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# CONTENTS

Contents.....	iii
New Taxa .....	v
Author Index .....	vi
ARTICLE	
1. The Middle Eocene Arshanto Fauna (Mammalia) of Inner Mongolia. Tao Qi .....	1
2. Ecology of small mammals in a gallery forest of central Brazil. Leslie Zuhn Nitikman and Michael A. Mares .....	75
3. Reproduction in a Spanish population of <i>Acanthodactylus erythrurus</i> (Reptilia: Lacertilia: Lacertidae). Stephen D. Busack and Lorrie L. Klosterman .....	97
4. Karyotypic analysis of five rodents and a marsupial from Belize, Central America. David W. Burton, John H. Bickham, Hugh H. Genoways, and Timothy J. McCarthy.....	103
5. Biosystematic studies in <i>Stenanthium</i> (Liliaceae-Veratreae). I. Floral morphology, floral vascular anatomy, geography and taxonomy of <i>S. occidentale</i> A. Gray. Frederick H. Utech .....	113
6. Results of The Carnegie Museum of Natural History Expeditions to Belize. II. Distributional notes on the birds of Belize. D. Scott Wood and Robert C. Leberman....	137
7. A review of the crane flies in the Subgenus <i>Tipula</i> ( <i>Papuatipula</i> ) (Diptera: Tipulidae), with descriptions of five new species. Chen W. Young.....	161
8. Taxonomic and geographic variation of <i>Liophis typhlus</i> and related "green" species of South America (Serpentes: Colubridae). James R. Dixon .....	173
9. A new species of <i>Clinidium</i> Kirby (Coleoptera: Carabidae or Rhysodidae) from Mexico, and descriptions of the females of two neotropical members of the genus. Ross T. Bell and Joyce R. Bell.....	193
10. Biosystematic studies in <i>Stenanthium</i> (Liliaceae-Veratreae). II. Floral morphology, floral vascular anatomy, geography and taxonomy of the Mexican <i>S. frigidum</i> (Schlecht. & Cham.) Kunth. Frederick H. Utech .....	197
11. Systematics of African bats of the Genus <i>Eptesicus</i> (Mammalia: Vespertilionidae). 2. Karyotypes of African species and their generic relationships. Karen McBee, Duane A. Schlitter and R. Laurie Robbins .....	213
12. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 8. First fossil lizard egg (?Gekkonidae) and list of associated lizards. Karl F. Hirsch, Leonard Krish-talka and Richard K. Stucky .....	223
13. Taxonomic notes on some African warblers (Aves: Sylviinae). Kenneth C. Parkes ...	231
14. <i>Spergenaspis</i> : a new Carboniferous trilobite genus from North America. David K. Brezinski .....	245
15. Decompression syndrome in fossil marine turtles. Bruce M. Rothschild .....	253
16. Towards a postglacial history of the northern Great Plains: A review of the paleoecologic problems. Cathy W. Barnosky, Eric C. Grimm and H. E. Wright, Jr.....	259
17. Fossil crab (Decapoda: Brachyura) fauna from the Late Cretaceous (Campanian-Maastrichtian) Pierre Shale in Bowman County, North Dakota. Annette B. Tucker, Rodney M. Feldmann, F. D. Holland, Jr. and Kenneth F. Brinster.....	275

18. Excavations at the Harney Site slave cemetery Montserrat, West Indies. David R. Watters..... 289

19. Description of skeletal remains from a Black slave cemetery from Montserrat, West Indies. Robert W. Mann, Lee Meadows, William M. Bass and David R. Watters.. 319



# NEW TAXA

## DESCRIBED IN VOLUME 56

NEW GENERA, SPECIES, AND SUBSPECIES

† <i>Sinosinopa</i> , new genus, Mammalia, Insectivora	15
† <i>Sinosinopa sinensis</i> , new species, Mammalia, Insectivora	15
† <i>Asiomys</i> , new genus, Mammalia, Rodentia	17
† <i>Asiomys dawsoni</i> , new species, Mammalia, Rodentia	18
† <i>Metacoryphodon</i> , new genus, Mammalia, Pantodonta	23
† <i>Metacoryphodon luminis</i> , new species, Mammalia, Pantodonta	23
† <i>Metacoryphodon? minor</i> , new species, Mammalia, Pantodonta	26
† <i>Pantolambdodon? minor</i> , new species, Mammalia, Pantodonta	28
† <i>Gobiatherium? major</i> , new species, Mammalia, Dinocerata	31
† <i>Gobiatherium? monolobotum</i> , new species, Mammalia, Dinocerata	32
† <i>Homogalax reliquius</i> , new species, Mammalia, Perissodactyla	33
† <i>Heptodon minimus</i> , new species, Mammalia, Perissodactyla	34
† <i>Heleletes medius</i> , new species, Mammalia, Perissodactyla	37
† <i>Hyrachyus neimongoliensis</i> , new species, Mammalia, Perissodactyla	39
† <i>Hyrachyus crista</i> , new species, Mammalia, Perissodactyla	42
† <i>Teleolophus primarius</i> , new species, Mammalia, Perissodactyla	54
† <i>Teleolophus? rectus</i> , new species, Mammalia, Perissodactyla	54
† <i>Microtitan? elongatus</i> , new species, Mammalia, Perissodactyla	59
† <i>Forstercooperia huhebulakensis</i> , new species, Mammalia, Perissodactyla	61
<i>Tipula</i> ( <i>Papuatipula</i> ) <i>insperata</i> , new species, Insecta, Diptera	164
<i>Tipula</i> ( <i>Papuatipula</i> ) <i>koiari</i> , new species, Insecta, Diptera	164
<i>Tipula</i> ( <i>Papuatipula</i> ) <i>nigritus</i> , new species, Insecta, Diptera	167
<i>Tipula</i> ( <i>Papuatipula</i> ) <i>oneilli</i> , new species, Insecta, Diptera	168
<i>Tipula</i> ( <i>Papuatipula</i> ) <i>wibleae</i> , new species, Insecta, Diptera	170
<i>Clinidium</i> ( <i>Mexiclinidium</i> ) <i>reyesi</i> , new species, Insecta, Coleoptera	193
<i>Cisticola chiniana keithi</i> , new subspecies, Aves	235
<i>Cisticola chiniana mbeya</i> , new subspecies, Aves	238
<i>Sylvietta leucophrys arileuca</i> , new subspecies, Aves	242
† <i>Spergenaspis</i> , new genus, Arthropoda, Trilobita	247
† <i>Spergenaspis salemi</i> , new species, Arthropoda, Trilobita	248
† <i>Spergenaspis easleyi</i> , new species, Arthropoda, Trilobita	250

† Fossil taxa.

## AUTHOR INDEX

Barnosky, C. W. ....	259
Bass, W. M. ....	319
Bell, J. R. ....	193
Bell, R. T. ....	193
Bickham, J. H. ....	103
Brezinski, D. K. ....	245
Brinster, K. F. ....	275
Burton, D. W. ....	103
Busack, S. D. ....	97
Dixon, J. R. ....	173
Feldmann, R. M. ....	275
Genoways, H. H. ....	103
Grimm, E. C. ....	259
Hirsch, K. F. ....	223
Holland, F. D., Jr. ....	275
Krishtalka, L. ....	223
Leberman, R. C. ....	137
Mann, R. W. ....	319
Mares, M. A. ....	75
McBee, K. ....	213
McCarthy, T. J. ....	103
Meadows, Lee. ....	319
Nitikman, L. Z. ....	75
Parkes, K. C. ....	231
Qi, T. ....	1
Robbins, R. L. ....	213
Rothschild, B. M. ....	253
Schlitter, D. A. ....	213
Stucky, R. K. ....	223
Tucker, A. B. ....	275
Utech, F. H. ....	113, 197
Watters, D. R. ....	289, 319
Wood, D. S. ....	137
Wright, H. E., Jr. ....	259
Young, C. W. ....	161







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ARTICLES 1-2

## CONTENTS

- |         |  |   |    |
|---------|--|---|----|
| Art. 1. | The Middle Eocene Arshanto Fauna (Mammalia) of Inner Mongolia .....  | Tao Qi                                    | 1  |
| Art. 2. | Ecology of small mammals in a gallery forest of Central Brazil ..... | Leslie Zuhn Nitikman and Michael A. Mares | 75 |

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**THE CARNEGIE**  
MUSEUM OF  
NATURAL HISTORY



THE MIDDLE EOCENE ARSHANTO FAUNA (MAMMALIA)  
OF INNER MONGOLIATAO QI<sup>1</sup>Visiting Museum Specialist  
Section of Vertebrate Fossils

## ABSTRACT

Review of the Eocene deposits in Inner Mongolia has shown that the classic "Arshanto Formation" forms the lower beds of the Irdin Manha Formation. Mammalian faunas from the Arshanto beds as well as from the overlying Irdin Manha beds are middle Eocene in age, roughly equivalent to the early and late Bridgerian, respectively. Two other units, formerly included in the "Arshanto Formation" are the Lower Eocene Bayan Ulan beds and the Upper Paleocene Nomogen beds, both here referred to the Nomogen Formation. Comparisons between the Inner Mongolian Arshanto fauna and the approximately time equivalent faunas of eastern and southern Asia suggest the existence of two Asiatic paleobiogeographic districts during the middle Eocene.

## INTRODUCTION

From 1975 to 1981 a team of specialists on the early Tertiary from the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, explored the Paleogene sediments in the Shara Murun region, Inner Mongolia, where the Central Asiatic Expedition of the American Museum of Natural History had made a series of investigations between 1922 and 1930. The team found approximately one hundred species of fossil mammals. Of these, a few were found by geologists mapping Inner Mongolia whereas others were recovered by the staffs of the Inner Mongolian Museum and the Institute of Vertebrate Paleontology and Paleoanthropology. Most of the discussions in this paper are based on these newly discovered fossils, although some previously collected specimens from the Arshanto fauna also are included.

The earliest report on an Asiatic middle Eocene fossil mammal (*Schlosseria magister*) was made by Matthew and Granger in 1926, but discoveries of fossil mammals of this age since that time have been rare. From the late 1950s to the present, new discoveries have been made in south Asia (Pakistan and India), central Asia (Kazakhstan), and east Asia (China) which have enhanced, considerably, our knowledge of middle Eocene mammalian faunas in Asia. The Arshanto fauna of China has a prominent position among these faunas, and the Arshantan Age has been designated as the Asiatic middle Eocene (Romer, 1966).

Study of the Arshanto has led us to the following conclusions:

1. The classic "Arshanto Formation" can be divided into three beds: the Upper Paleocene Nomogen beds, the Lower Eocene Bayan Ulan beds, and the Middle Eocene Arshanto beds. In 1975, the Nomogen mammalian fauna was discovered in Haliut and Gonghutong (Zhou and Qi, 1978) in strata at the lowest level of the classic "Arshanto Formation," but the boundary between the "Arshanto beds" and the underlying "Nomogen beds" was not clear. In 1976, another mammalian

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fauna (under study by Zhai), which is quite similar to but shows some differences from the Nomogen fauna, was found in Bayan Ulan above the level of the Nomogen beds. Fossil mammals also were found in the Arshanto beds in several other areas such as Arshanto Obo, Irdin Manha, Bayan Ulan, Huhe Bulak, and Ulan Bulak in 1976 and 1977. These are the main materials described in this paper, and these faunas comprise the Arshanto fauna.

2. The composition of the Arshanto fauna bears some resemblance to that of the Irdin Manha fauna. The ages of both are close, i.e., middle Eocene. Therefore, three middle Eocene mammalian faunas are recognized in the eastern part of China: the earliest, Xintai (Sintai) fauna (Zhou and Qi, 1982), the Arshanto fauna, and the latest, Irdin Manha fauna. The Arshanto and Irdin Manha faunas are quite different from the Inner Mongolian Shara Murun fauna in composition. The age of the latter is unquestionably late Eocene, on the basis of such mammals as the hyaenodontid *Pterodon*, the perissodactyl *Deperetella*, and the artiodactyl *Archaeomeryx*.

3. The age of the Arshanto fauna seems to compare most closely with that of the early middle Eocene Bridger fauna (Bridger A and B) of North America, especially on the basis of the helaletids and the brontotheriids. It must be noted, however, that some elements of the Arshanto fauna are more typically associated with older faunas (*Harpagolestes*, *Homogalax*), whereas at least *Forstercooperia* is more typically younger.

4. Based on the known fossils, the east and central Asiatic middle Eocene faunas belong to the same paleogeographic district, and both are quite different from those of the south Asiatic district. The southern fauna has some marine mammals, such as Cetacea, and some terrestrial animals, such as Proboscidea and Artiodactyla, which never or very rarely appear in the Arshanto fauna and in central Asia. Some relatives (Anthracotheriidae) of middle Eocene mammals found in south Asia were discovered in late Eocene beds in south China and Burma, but are rare in northern Asia. Therefore, southern and southeast Asia appear to belong to another paleogeographic district.

Abbreviations used in this paper are: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology; AMNH, American Museum of Natural History; L, length; W, width; ant., anterior; post., posterior.

Older Chinese spelling (Wade-giles) is used in the bibliographic references through 1972, following the Bibliographies of Vertebrate Paleontology.

## GEOLOGY

### *Field Work (Fig. 1)*

Berkey and Morris (1924, p. 119) first mentioned the Arshanto beds (Formation) as follows: "At Irdin Manha, twenty miles southeast of Iren Dabasu, the Houldjin is not found, and the section exposed consists of 40 to 100 feet of grey sands, with a rich titanothera fauna, which may be late Middle Eocene or even Upper Eocene. Beneath the titanothera beds there are red clays, provisionally called Arshanto, and probably to be correlated with the barren beds above the Iren Dabasu. The Arshanto may prove to be only the lower Irdin Manha, or it may be separated from the Irdin Manha by a disconformity. The base of these beds has not been seen."

In their study of *Schlosseria magister* and *Teilhardia pretiosa*, Matthew and Granger (1926, p. 1) said, "At the base of the Irdin Manha and Shara Murun formations are red clays generally barren, to which Berkey and Morris have given

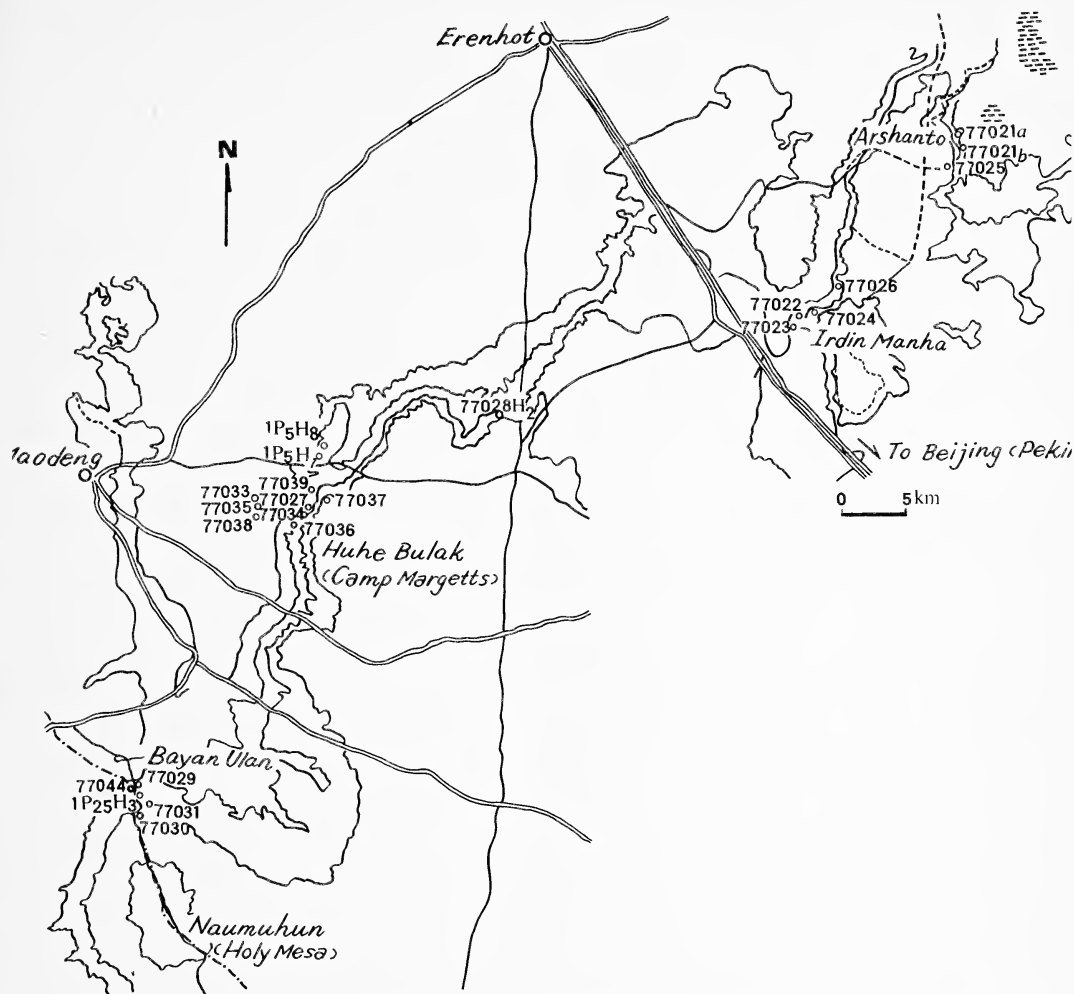


Fig. 1.—Map of Inner Mongolian Paleogene localities ("Naumuhun" = Nomogen in text).

the provisional name of Arshanto formation. The only fossils found are two remarkable little perissodactyls, apparently related to the lophiodontoid genera of the Irdin Manha and Ardyn Obo, but much more primitive. As far as the evidence goes the Arshanto may be Middle Eocene, but there is no correlation apparent with any Middle Eocene mammals of Europe or North America."

Later, Berkey and Morris (1927, p. 207) described the Arshanto beds in detail: "The Arshanto beds are prevailing red clays and fine silts, which, on weathering, crumble into small hard chips. Much of the deposit is structureless, almost like loess. In some places a faint color-banding is seen in the red beds, but no shaly structure or marked bedding. Color-banding is held by Matthew (1915, pages 395–398) to be not inconsistent with wind deposits, and our observations tend to support his opinion. In still other places, chocolate brown beds and, more rarely, thin grey layers appear among the red, and here at least there is definite bedding. About a mile east of Irdin Manha escarpment lies another broad, un-

drained hollow (Fig. 99, page 198), part of which is called Arshanto, from which the formation is named. Here some lense-shaped beds of grey and red sandstone were found in the red clays. A limited collection of small lophiodonts was made, which has not yet been fully studied; but the preliminary examination by Matthew and Granger shows that they are quite different from the lophiodonts of the Irdin Manha beds. The base of the red beds was not seen, the only bottom known for the formation is at Iren Dabasu, where it rests upon the Cretaceous beds."

Radinsky (1964, p. 3) considered the age of the Arshanto beds early late Eocene because, "*Schlosseria* is similar enough to *Lophialetes* to indicate only a very slightly older age, possible early Late Eocene, for the Arshanto beds." Later, Radinsky (1965, p. 201) pointed out again, "*Schlosseria magister* is probably not much older than *Lophialetes expeditus* and on morphological grounds could equally well be late Middle Eocene or early Late Eocene in age." Romer (1966) took the "Arshanto Age" to designate the Asiatic middle Eocene age.

In 1975, after representative late Paleocene mammals were found by an Inner Mongolian geological mapping team, Zhou and Qi (IVPP) studied the localities and suggested on the basis of field evidence that these late Paleocene mammal-bearing beds were in the Arshanto Formation (Zhou et al., 1976). In August, 1976, paleontologists of the IVPP found fossil mammals, later named the "Bayan Ulan fauna," at Bayan Ulan, which is located on the north slope of the Nomogen Mesa. Above these Bayan Ulan beds are the Arshanto beds, which in turn are overlain by the Irdin Manha beds. The Arshanto beds yielded some middle Eocene mammals including *Gobiatherium mirificum* and *Hyrachyus cristata* new species.

In June 1977, the IVPP team discovered the incisors of *Gobiatherium mirificum*, the premolars of insectivores, and some teeth of lophialetids (field nos. 77023, 77026) at Arshanto Obo. Approximately thirty more taxa of fossil mammals were found in the Arshanto beds at Huhe Bulak and Bayan Ulan, and ten or more kinds of early Eocene fossil mammals were recovered at Bayan Ulan. Two small collections were made in these areas by the IVPP in 1978 and 1980.

### *Irdin Manha Formation and Arshanto Beds*

Granger and Berkey (1922) proposed using "Irdin Manha Formation" for a set of grey-white sandstone beds (bearing numerous titanotheres) 25 miles south of Iren Dabasu salt lake. Thickness of the beds ranges between 40 and 100 feet. The age of the beds was considered to be Eocene-Oligocene. Later, Berkey and Morris (1924) pointed out that the age of the Irdin Manha Formation may be late middle Eocene or late Eocene. At this time they mentioned a red clay below the "titanotheres beds" and, as mentioned above, gave the provisional name, Arshanto, to the red bed.

Since 1926, when Matthew and Granger described *Schlosseria magister*, the "Arshanto fauna" was little studied until field work, mostly between 1975 and 1978, again produced many fossil mammals. These discoveries, as well as others in south Asia, central Asia, and other parts of China (Shandong and Henan provinces and Xinjiang Uighur Autonomous Region) have contributed a great deal to understanding the middle Eocene Asiatic mammalian faunas, and the Arshantan Age as an important time in geological and mammalian history.

The "Arshanto Formation" of Berkey and Morris (1927, p. 206) can be divided into two parts: the upper part, named "Arshanto beds," is here included as the lower part of the Irdin Manha Formation; the lower part of Berkey and Morris'

"Arshanto Formation" is the Nomogen Formation and contains two levels: the upper Lower Eocene Bayan Ulan beds and the lower Upper Paleocene Nomogen beds (or celestite-nodule bearing beds).

The thickness of the Irdin Manha beds is variable: at Huhe Bulak, only 5.4 m; at Bayan Ulan, 41 m; at Arshanto Obo, 10 m; and at Irdin Manha and Ulan Shireh, 12–30 m and 43 m respectively. It changes rapidly over a short distance and indicates topography at the time of deposition. In spite of the existence of an erosional surface between the Irdin Manha beds and the Arshanto beds in some places, the general characters of the two beds are quite similar. Therefore, the two beds are regarded as composing the Irdin Manha Formation. The Arshanto beds are found mainly in Sunid Yuqi (county). Their northeast extent is located near Arshanto Obo and their southwest boundary occurs at Nomogen Mesa.

Below the Irdin Manha beds in Aliusu, Urtyn Obo area, there is a set of dark red clay beds. These were previously considered Arshanto beds, but are perhaps best referred to the Nomogen Formation. They bear a pantodont, *Pastoralodon lacustris*, which is otherwise known only in the upper part of the Nomogen Formation in the Bayan Ulan fauna.

The following are abbreviated geological sections (numbers in parentheses are IVPP field numbers).

#### I. Arshanto Obo section (upper to lower Fig. 2)

##### **Irdin Manha Formation**

##### Middle Eocene Irdin Manha beds

- 4) upper part: grey-green, grey-yellow sandstone to the top having a light red medium sandstone and tobacco-yellow medium quartz sandstone with coarse quartz gravels (diameter generally less than 1 cm, the maximum 3 cm); grains rounded, but not well sorted and not well bound.  
lower part: grey-green and grey-yellow medium and fine sandstone, well bound together by siliceous cement; fine silt-sandstone can often be seen in the transverse direction; locally having numerous muddy clumps, *Forstercooperia confluens* (77025). 10.13 m

——disconformity (base of channel)——

##### Middle Eocene Arshanto beds

- 3) dark red clay with few muddy clumps and fine silica grains, not well bound. 2.05 m
- 2) upper part: being covered by Quaternary plants. 13.94 m  
middle part: grey-green sandstone, mainly silica grains, bound by siliceous cement.  
lower part: variegated sandstone (mainly grey color; secondary dark red) with numerous muddy clumps at base bearing *Gobiathe-rium mirificum*, *Schlosseria magister*, etc. (77021). 16.88 m
- 1) dark red sandy clay with few muddy clumps. 1.68 m

——bottom not visible——

#### II. Huhe Bulak section (Fig. 3)

##### **Irdin Manha Formation**

##### Middle Eocene Irdin Manha beds

- 1) grey-white on surface, but grey-yellow inside, sandstone and sandy gravels with many cylinder-like calcareous masses; having grey sandy conglomerate and sandstone; gravels often black quartz, the diameter 1 cm or so, with *Andrewsarchus* (= *Paratriisodon*; McKenna, personal communication) *gigas*, etc. (77037). 5.4 m

——unconformity (=base of channel)——

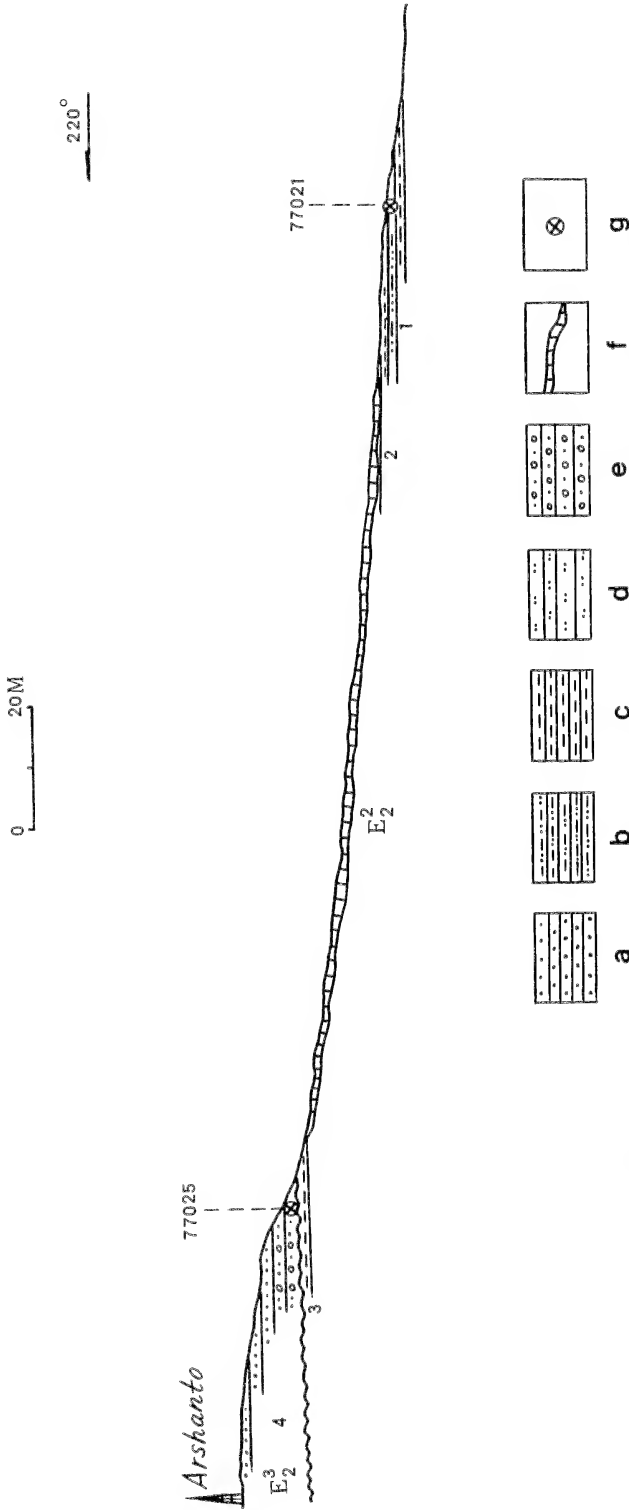


Fig. 2. — Arshanto section. (a) coarse sandstone; (b) stiltstone; (c) mud stone; (d) sandstone; (e) conglomerate; (f) Quaternary cover; (g) fossil mammal locality. "E" with numerical superscript or subscript are Chinese mapping symbols that denote divisions of the Paleogene.



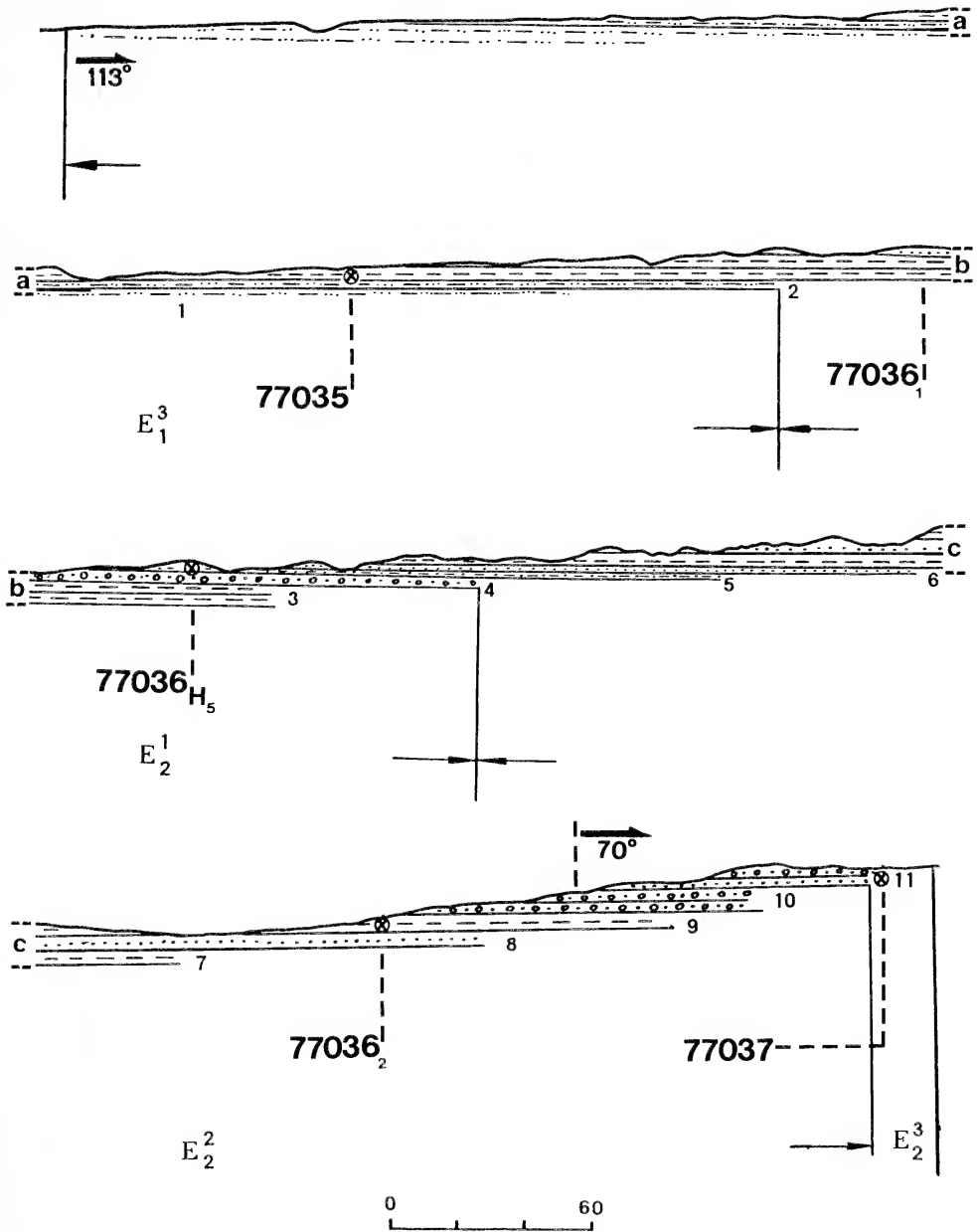


Fig. 3.—Huhe Bulak section (in 4 segments, top to bottom; complete horizontal section connects at a, b, c). See legend in Figure 2.

Middle Eocene Arshanto beds

- 10) top: dark grey-green-pink sandy clay.  
upper part: yellow-green fine sandstone.  
bottom: grey-green sandy “conglomerates” (“gravels” mainly being muddy masses and quartz, etc., diameter 0.2 cm), with *Gobia-*

- therium mirificum*, *Mesonyx obtusidens*, *Schlosseria magister*, etc. (77036-2). 6.0 m
- 9) upper part: dark red clay with fossil mammal fragments and calcareous-nodules, diameter 1.5 cm. 4.04 m  
lower part: brown clay with few manganese nodules. 0.3 m
- 8) red-grey muddy siltstone (white on surface), with few mammalian incisors and fragments (77036-H8). 4.85 m
- 7) brown-loess-red clay, with manganese nodules, the diameter 0.5 cm; bearing few limb bones of Dinocerata (77036-H7). 5.1 m
- 6) light loess-red siltstone. 0.3 m
- 5) brown muddy siltstone (white on surface) with few calcareous nodules, bearing *Sinosinopa sinensis* (77036-H5). 2.0 m
- 4) brown-grey sandy conglomerates (grey on surface), gravels mainly a lot of muddy masses and colorless, black, or yellow-green quartz grains, with many fossil tapirs, fragments of turtles and crocodiles. Fining upward. 3.04 m
- 3) dark red or grey-green variegated clay, with few quartz grains and calcareous nodules, bearing astragali of Dinocerata (77036-H3). Grey-green clay decreased and manganese nodules apparent up section. 6.5 m

——disconformity——

### Nomogen Formation

Lower Eocene Bayan Ulan beds

- 2) brick-red sandy clay with few nodules and many bone fragments, bearing fossil tapirs, Dinocerata (*Prodinoceras* sp. = *Mongolotherium*; McKenna, personal communication) (77035). 2.76 m
- 1) loess-red and grey-green clay with many calcareous nodules between 5–10 cm diameter. 3.0 m

——base not visible——

### III. Bayan Ulan sections (after material of the Inner Mongolian mapping team; Fig. 4)

#### Ulan Gochu Formation

Oligocene

- 17) loose coarse sandstone with gravels with fragments of cf. *Indri-cotherium* sp. (1P<sub>25</sub>H<sub>19</sub>). 6.6 m
- 16) variegated clay. 2.6 m
- 15) grey-white medium feldspar-quartz bearing sandstone with *Teleolophus magnus*. 0.5 m
- 14) brown-red clay. 1.8 m
- 13) grey-white silt-sandstone. 3.3 m
- 12) grey-white medium feldspar-quartz bearing sandstone. 4.8 m
- 11) light brown-red clay. 1.6 m
- 10) grey-white coarse sandstone with gravels. 0.3 m

——disconformity——

#### Irdin Manha Formation

Middle Eocene Irdin Manha beds

- 9) brown-red clay with *Gobiohyus* sp., ?*Harpagolestes* sp. and Mesonychidae indet. (1P<sub>25</sub>H<sub>11</sub>). 27.5 m
- 8) loose manganese sandy conglomerates and loose medium-coarse sandstone. Upper part: grey-white, light yellow medium feldspar-quartz bearing sandstone with *Teleolophus* sp., *Microtitan mongoliensis*, and *Lophialetes* sp. 6.9 m
- 7) variegated silty clay, with *Microtitan mongoliensis*, *Lophialetes* sp., *Eudinoceras* sp., and *Rhodopagus* sp. (1P<sub>25</sub>H<sub>7</sub>). 6.7 m

——disconformity——

Middle Eocene Arshanto beds

- 6) brown-red clay with grey-green clay, with *Rhodopagus* sp., and *Lophialetes* sp. 10 m

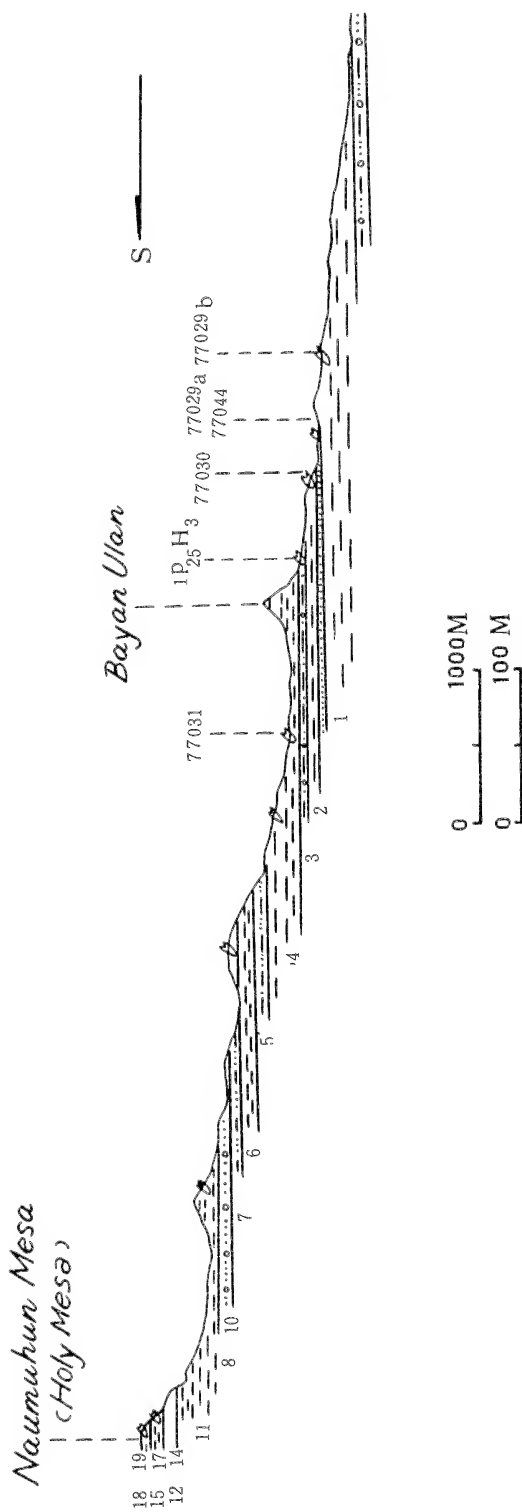


Fig. 4.—Bayan Ulan section (Holy Mesa area). See legend in Figure 2. Upper scale, horizontal; lower scale, vertical.

- 5) grey-green silty clay. 2.9 m
- 4) brown-red clay with grey-green siltstone and grey-green clay, bearing ?*Mongolonyx prominentis*, *Hyrachyus cristata*, *Breviodon minutus*, *Pantolambdodon* sp., and *Lophialetes* sp. 25 m
- 3) gravel-bearing brown-red clay with green clay and siltstone, the bottom is brown sandy conglomerates, bearing *Gobiatherium monolobatum* (1P<sub>25</sub>H<sub>3</sub>). 4 m

——disconformity——

#### Nomogen Formation

##### Lower Eocene Bayan Ulan beds

- 2) variegated clays with *Prionessus lucifer*, *Mimotona borealis*, *Pseudictops lophiodon*, *Pachyaena* sp., *Plagiocristodon serratus* (milk teeth of *Dissacus*, McKenna, personal communication), *Pastoralodon lacustris*, *Prodinoceras* (= *Mongolotherium*; McKenna, personal communication) *efremovi*, *Prodinoceras* (= *Mongolotherium*) sp., *Pyrodon* sp., *Palaeostylops iturus*, *Palaeostylops macrodon*, *Mongolotherium* sp., and ?*Lambdotherium* sp. 6.5 m
- 1) brown-red sandy-silty sandstone, grey-green silty clay appears in the top. Bottom: grey-white silty clay with gravels and red muddy sandstone with gravels, bearing *Pastoralodon lacustris*, *Prionessus lucifer*, *Sarcodon pygmyaeus*, *Palaeostylops iturus*, and *Pantolambdodontidae* (new genus and species), etc.

——bottom not visible——

#### FOSSIL MAMMALS FROM ABOVE AND BELOW THE ARSHANTO BEDS

##### I. The Overlying Irdin Manha Beds

The Irdin Manha fauna has been collected from at least ten sites, of which four are major: the Irdin Manha escarpment, Ulan Shireh, Aliusu, and Camp Margetts.

1. Irdin Manha escarpment. This site is located 40 km south of Iren Dabasu salt lake on the southwest edge of Suji Mesa. This is the type area of the Irdin Manha Formation and has been called by various authors "Irdin Manha Formation," "Irdin Manha beds," "Irdin Manha area," and "near Irdin Manha." The thickness of the type Irdin Manha beds is 41 m and the fossil quarry (a titanotherium site excavated by Russian paleontologists) is not far above the Arshanto beds. Appendix 1 lists the fauna from this site.

2. Ulan Shireh. The fossil quarry is located 10 km northeast of Tukhum Lamasary (Siziwangqi). No fossil mammals were discovered in other beds at this site.

3. Aliusu. This fossil quarry was found in 1975 by the staff of the Inner Mongolian mapping team and the author. It is located in the Urtyn Obo area. These beds appear to be correlatives of the type Irdin Manha beds, and preserve the following fossil mammals:

##### Rodentia

*Adenimus* sp.

##### Creodonta

*Propterodon* sp.

##### Pantodonta

*Eudinoceras mongoliensis*

*Pantolambdodon inermis*

##### Acreodi

?*Harpagolestes orientalis*

##### Perissodactyla

*Protitan grangeri*  
*Microtitan mongoliensis*  
*Microtitan* sp.  
*Lophialetes expeditus*  
*Breviodon minutus*  
*Breviodon* sp.  
*Teleolophus medius*  
*Teleolophus* sp.  
*Forstercooperia confluens*  
*Artiodactyla*  
*Gobiohyus orientalis*  
*Dichobunid* sp.

4. Camp Margetts. Camp Margetts was located somewhere in the Ulan Bulak-Huhe Bulak escarpment, some kilometers to the west of the Irdin Manha escarpment. The AMNH Central Asiatic Expedition collected a few fossil mammals from two beds called "Houldjin beds" and the underlying "Irdin Manha beds" in this area. The discovery in 1978 of *Lophialetes expeditus* in the "Houldjin gravels" here proved that they represent a lateral facies of the type Irdin Manha beds, and should be considered part of the Irdin Manha Formation. The underlying "Irdin Manha beds" at Camp Margetts are probably equivalent to the Arshanto beds.

On the other hand, some AMNH fossils are labeled as coming from "7 miles (about 10 km) southwest of Camp Margetts," or "10 miles (17 km) west of Camp Margetts," or "5 miles (8 km) west of Camp Margetts." Among these sites, the "west" area may be the Bayan Ulan area. These sites cannot be correlated directly with the strata in the Camp Margetts area. However, we may guess the provenance of some fossil mammals by referring to those preserved in the type Irdin Manha and type Arshanto beds. Cf. *Hyrachyus* and *Helalestes* sp., for example, probably came from the Arshanto level, and *Forstercooperia confluens*, *Mongolonyx dolichognathus*, and *Litolophus* (*Grangeria*) *gobiensis* from Irdin Manha levels.

The fossil mammals from known localities in the Camp Margetts area are listed below (excluding the new mammals reported in this paper):

#### A. Irdin Manha level ("Houldjin beds")

Pantodonta  
*Hypercoryphodon thomsoni* Osborn, 1932  
 Condylarthra  
*Andrewsarchus* (= *Paratriisodon*) *gigas* (Qi, 1980)  
 Perissodactyla  
*Lophialetes expeditus* Radinsky, 1965  
*Brontotheriidae* indet. Qi, 1980

#### B. Arshanto beds

Rodentia  
 ?Paramyid sp. Dawson, 1964  
*Tamquammys wilsoni* Dawson, Li and Qi, 1984  
*Adenimys burkei* Dawson, 1964  
 Dinocerata  
*Gobiatherium mirificum* Osborn, 1932  
 Perissodactyla  
*Schlosseria* sp. cf. *Schlosseria magister* Radinsky, 1965  
*Helalestes fissus* Matthew and Granger, 1925  
*Helalestes fissus*? Radinsky, 1965  
*Metatelmatherium cristatum* Granger and Gregory, 1943  
*Protitan minor* Granger and Gregory, 1943

## II. The Underlying Bayan Ulan Beds

The following mammalian fauna of early Eocene age is found in these beds (Zhai, under study):

- Multituberculata
  - Prionessus lucifer*
- Anagalida
  - Mimotona borealis*
  - Pseudictops lophiodon*
- Notoungulata
  - Palaeostylops iturus*
  - P. macrodon*
- Acreodi
  - Pachyaena* sp.
  - Dissacus* (= *Plagiocristodon*) *serratus*
- Pantodonta
  - Pastoralodon lacustris*
- Dinocerata
  - Prodinoceras* (= *Mongolotherium*) *efremovi*
  - Prodinoceras* (= *Pyrodon*) sp.
- Perissodactyla
  - ?*Lambdotherium* sp.

### ASIATIC MIDDLE EOCENE MAMMALS

Asiatic middle Eocene mammals have been found in east Asia (China: Inner Mongolia, Shandong, and Henan; Mongolian People's Republic), central Asia (China: Xinjiang, and U.S.S.R.: Kazakh region), and south Asia (Pakistan and India). Areas yielding important discoveries are:

1. Central part of Shandong Province. After the original report (Zdansky, 1930), Young and Bein (1935) and Chow (1957, 1963) added more middle Eocene mammals. Zhou and Qi (1982) summarized the Shandong Eocene mammals, and Qi and Meng (1983) reported two other species of perissodactyls collected in Wufu County. Appendix 2 lists the middle Eocene mammals from central Shandong.

2. Henan Province. Zhou et al. (1975, p. 179) concluded of the Lushi fauna, "It is typically a southern extension of the Irđin Manha fauna (type locality), but contains some interesting forms which are not known in the Irđin Manha" (Appendix 1).

Gao (1976) divided the Paleogene in the Wucheng and Xichuan Basins, Henan, into four formations (lower to upper): 1) Yuhuangding Formation; 2) Dacangfang Formation; 3) Hetaoyuan Formation; and 4) Shangsi Formation. Only a coryphodontid and a dinoceratan were found in the Yuhuangding Formation, the age of which is considered to be, "not later than Middle Eocene." Fossil mammals found in the Dacangfang Formation are:

- Rodentia
  - Sciuravus* sp.
- Carnivora
  - Miacis* sp. aff. *M. invictus*
- Creodonta
  - ?*Sinopa* sp.
  - ?*Tritemnodon* sp.
- Acreodi
  - ?*Andrewsarchus* sp.
- Perissodactyla
  - Sianodon* sp.

*Teleolophus* sp. cf. *T. medius*

*Deperetella* new species

*Breviodon* sp. cf. *B. minutus*

*Lophialetes* sp.

*Colodon* sp.

?*Protitan* sp.

Tillodontia

*Chungchienia sichuanica*

Gao (1976) concluded that [translated from Chinese], "The age of the majority of the fossil mammals collected from Hetaoyuan Formation should be the same as the Irдин Manha fauna found in Inner Mongolia."

Accordingly, the Yuhuangding Formation may be tentatively correlated with the Guanzhuang Formation, the Dacangfang Formation with the Arshanto beds, and the Hetaoyuan Formation with the Irдин Manha beds.

3. U.S.S.R. Since the early 1960s, middle Eocene mammals have been reported from the Zaysan (Zaisan) Basin, Kazakh region (Appendix 3).

4. Pakistan and India. Following Pilgrim's description (1940) of middle Eocene mammals from North-west India, Dehm and Oettingen-Spielberg (1958) described the middle Eocene Ganda Kas fauna from Pakistan. Later, several studies reported on middle Eocene mammals from India and Pakistan (West, 1980, and Appendix 4).

Additional collections of possibly middle Eocene mammals have been made in southern provinces of China, including Yunnan, Guangxi, Hubei, and Jiangxi.

#### MIDDLE EOCENE FAUNAL ZONES IN EAST ASIA

There are three middle Eocene mammalian faunal zones in east Asia. From oldest to youngest, there are: 1) Guanzhuang faunal zone (Shandong Province); 2) Arshanto faunal zone (Inner Mongolia); and 3) Irдин Manha faunal zone.

*Hyrachyus modestus* collected from the Guanzhuang Formation also occurs in Bridger B beds in North America. The tillodont, *Kuanchuanianus shantunensis* (Chow, 1963), from Shandong resembles *Trogosus* and *Tillodon* (both lower Bridger; Stucky and Krishtalka, 1983). Accordingly, the age of the Guanzhuang and lower Bridger faunas may be comparable.

In the Arshanto fauna, *Hyrachyus* sp. cf. *H. eximius* is close to *Hyrachyus eximius* from the Bridger C and D. Other similar tapiroids, such as helaletids, occur in both faunas. This indicates that the Arshanto fauna is younger than the Guanzhuang fauna and closer in age to the upper Bridger fauna. *Homogalax*, a typical North American Greybullian tapir, survives as a relict in the middle Eocene Arshanto fauna of Asia.

Although the Guanzhuang and Arshanto faunas have certain endemic taxa, their composition suggests that faunal exchange took place during the early and late Bridgerian between east Asia and North America.

The Arshanto and the Irдин Manha faunas appear to be closely related. A main characteristic of the Arshanto fauna is the dominance of a variety of perissodactyls and the absence of artiodactyls. Of the 43 species in the Arshanto fauna, about 23 (53%) are perissodactyls. Perissodactyls still dominate the Irдин Manha fauna, but several new families appear: Leporidae, Oxyaenidae, Hyaenodontidae, Miacidae, and Amynodontidae(?).

The following species occur in both faunas: *Breviodon minutus*, ?*Forstercooperia grandis* and *Pantolambdodon fortis*. Genera in common are: *Hapalodectes*, *Mesonyx*, *Helaletes*, *Teleolophus*, *Protitan*, and *Telmatherium*. Importantly, phylo-

genetic relationships are evident between several taxa in the two faunas such as: *Schlosseria magister* and *Lophialetes expeditus*; *Helalestes medius* and *H. mongoliensis*; *Telmatherium cristatum* and *T. parvum*; *Protitan minor* and *P. robustus*; and *Metacoryphodon*, *Eudinoceras*, and *Hypercoryphodon*.

The similarities between the Arshanto and Irдин Manha faunas are in contrast to the differences between the latter and the Shara Murun fauna. There are only three shared genera (*Shamolagus*, *Rhodopagus*? and *Triplopus*?) in the Irдин Manha and Shara Murun faunas, and no shared species. There are some phylogenetic relationships between several species such as *Teleolophus medius* and *Deperetella cristata*, and *Forstercooperia confluens* and *Juxia sharamurunensis*, as well as within the Rodentia and Lagomorpha. But in the Shara Murun fauna, brontotheres and artiodactyls (mainly *Archaeomeryx optatus*) are dominant, whereas they are absent from the Irдин Manha fauna. The appearance of the Family Anthracotheriidae in the Shara Murun fauna marks the beginning of the late Eocene in China.

East Asia and central Asia were in the same paleobiogeographic district (North Paleobiogeographic District) during the middle Eocene. The central Asian middle Eocene mammalian faunas occur mainly in the Kazakh and Kirgizia regions, U.S.S.R., and in Xinjiang, China, but correlating these faunas is difficult. The fauna from Xinjiang appears to be equivalent to the Irдин Manha fauna. The central Asian faunas are generally similar in composition to those of east Asia, and may represent extensions of the eastern Arshanto and Irдин Manha faunas, although not of the Guanzhuang fauna. Middle Eocene genera common to central and eastern Asia are: *Lophialetes*, *Helalestes*, *Teleolophus*, *Forstercooperia*, *Triplopus*, *Pataecops*, *Eudinoceras*, and *Tamquammys*.

South Asia was another paleobiogeographic district (South Paleobiogeographic District) in the middle Eocene. At present, the Qinghai-Tibetan plateau stands between east-central Asia and south Asia. During the middle Eocene, at least during a large part of that time, Tethys lay, in part, between the two. Recent discoveries do not support the assumption that south Asia and east-central Asia were in the same paleobiogeographic district. Unquestionably there were some links between the two areas. Some genera such as *Schlosseria*, *Teleolophus*, *Forstercooperia*, and *Tamquammys* were shared between south Asia and east Asia, but there are considerable differences at the specific level between the two regions. The appearance of *Gobiohyus orientalis* in the two areas indicates that the age of the south Asian faunas is, in part, equivalent to that of the Irдин Manha fauna and that during the time of the Irдин Manha fauna the eastern part of the Tethys Sea had already closed, allowing exchange of some mammals.

Finally, Sahni et al. (1981, p. 693) pointed out that the middle Eocene south Asian fauna "includes perissodactyls and rodents, most of them being endemic at the generic level, showing strong and indubitable affinities to the Eocene faunas of Northern Asia, Mongolia and Kazakhstan. The diversity among these groups and the endemism of the taxa strongly suggest an Early Eocene immigration from the North." A recent study of the origin of the proboscideans (Domning et al., 1986) suggests, however, another route for faunal migration between south-east Asia and south Asia, namely, a South China-Burma-Indo-Pakistan route.

#### SYSTEMATIC PALEONTOLOGY OF THE ARSHANTO FAUNA

The discoveries of the Arshanto fauna are centered in the Shara Murun area, i.e., 110°30' to 112°30'E; 43°00' to 43°40'N. Most of the fossil mammal sites are located in Sunid Yuqi (county) of Ulan Chabu Mong, Inner Mongolia.



Grandorder Insectivora Illiger, 1811  
 Order Soricomorpha Gregory, 1910  
 Superfamily Palaeoryctoidea Winge, 1917  
 Family Micropternodontidae Stirton and Rensberger, 1964  
*Sinosinopa*, new genus

*Type species.*—*Sinosinopa sinensis*, new genus, new species.

*Included species.*—Type and only species.

*Diagnosis.*—Retains  $M_3^1$  unlike *Prosarcodon* and *Sarcodon*;  $P_4$  more elongate and  $M^{1-2}$  with larger hypocone shelf.

*Sinosinopa sinensis*, new species

(Fig. 5; Table 1)

*Holotype.*—V5677, incomplete skull and mandible, with left  $P^1$ – $M^3$ , right  $C^1$ – $P^4$  ( $M^{1-2}$  broken), and left  $M_{2-3}$  (field no. 77036-H<sub>5</sub>).

*Diagnosis.*—Dental formula  $?/?$ ,  $1/?$ ,  $4/?$ ,  $3/3$ ; large in size; diastema very short; nasal bone elongate; post-metacrista fairly long; hypocone shelf (talon basin) very wide;  $M^3$  with two paraconules; trigonids and talonids well developed; trigonid of  $M_3$  very long; metaconulid fairly prominent.

*Description.*—Skull: ascending ramus of premaxilla present; maxilla relatively high and long; nasal bone very elongate, its posterior edge above  $M^1$ ; frontal bone relatively broad; orbit large; infraorbital foramen fairly small; zygoma not deep (posterior part broken); palatine part of maxilla very long; and foramen incisivum fairly large.

Upper teeth.  $C^1$ : relatively robust; transverse section oval; postcanine diastema fairly short.  $P^1$ : smallest in size; compressed anteroposteriorly; one main cusp, anterior edge of cusp relatively steep.  $P^2$ : larger in size; anterior edge of main cusp less steep than that of  $P^1$ , posterior edge also gentle; cuspule on posterior edge of tooth, but not clear.  $P^3$ : crown view triangular; paracone and protocone clear; small cuspule (parastyle) on anterior edge of tooth; another larger cuspule (metastyle) on posterior edge.  $P^4$  (paracone and metacone broken): becoming molariform; protocone prominent; pre-protocrista and post-protocrista clear, forming a narrow trigon basin; hypocone relatively prominent; hypocone shelf very narrow; parastyle small, relatively prominent; metastyle prominent, but not extending very far posteriorly.  $M^1$ : protocone prominent; pre-protocrista and post-protocrista not prominent; pre-paraconule crista relatively clear; post-paraconule crista not clear; trigon basin narrow; parastyle and metastyle (crowns broken) forming a “V”-shaped ectoflexus (sharp at bottom of “V,” and anterior wing of “V” longer than posterior wing); a small cingulum in front of paraconule; trigon basin wide; a prominent hypocone and another small cusp on postero-lingual edge of trigon basin.  $M^2$ : post-metacone crista (broken) probably fairly elongate; protocone prominent; trigon basin narrow; paraconule larger than metaconule; pre-paraconule crista less clear than that of  $M^1$ ; stylar shelf narrow; parastyle cone-like; metastyle relatively elongate; ectoflexus opening largely; small segment of cingulum anterior to paraconule; trigon basin wide; prominent hypocone and another cuspule at postero-lingual edge of trigon basin.  $M^3$ : protocone prominent; pre-protocrista and post-protocrista clear; with two paraconules, one on lingual side smaller than other; trigon basin wide; paracone close to metacone; paracone high; no metastyle, cingulum, and hypocone.

Mandible: horizontal ramus slender; anterior edge of ascending ramus relatively steep; anterior edge of masseteric fossa at rear of  $M_3$ .

Lower cheek teeth.  $P_4$  (main cusp broken): anterior and posterior cuspules clear; section of crest in posterior part of tooth.  $M_1$ : (only two roots left).  $M_2$ : trigonid and talonid clear, length almost same; protoconid-paraconid-metaconid forming distinct trigonid; carnassial notch between protoconid and paraconid stronger than that between protoconid and metaconid; positions of hypoconid, entoconid, and hypoconulid somewhat posterior; cristid obliqua between hypoconid and protoconid relatively strong; small cingulum on antero-labial side of paraconid.  $M_3$ : talonid narrow and elongate, hypoconulid very prominent; distance between hypoconid and entoconid, and hypoconulid longer than on  $M_2$ ; cristid obliqua stronger.

*Discussion.*—When Matthew and Granger (1925a) described the genus *Sarcodon*, only  $M^1$  was known. Its systematic position was uncertain until Szalay and McKenna (1971, pp. 286–293) recognized the lower teeth of *Opisthopsalis vetus*

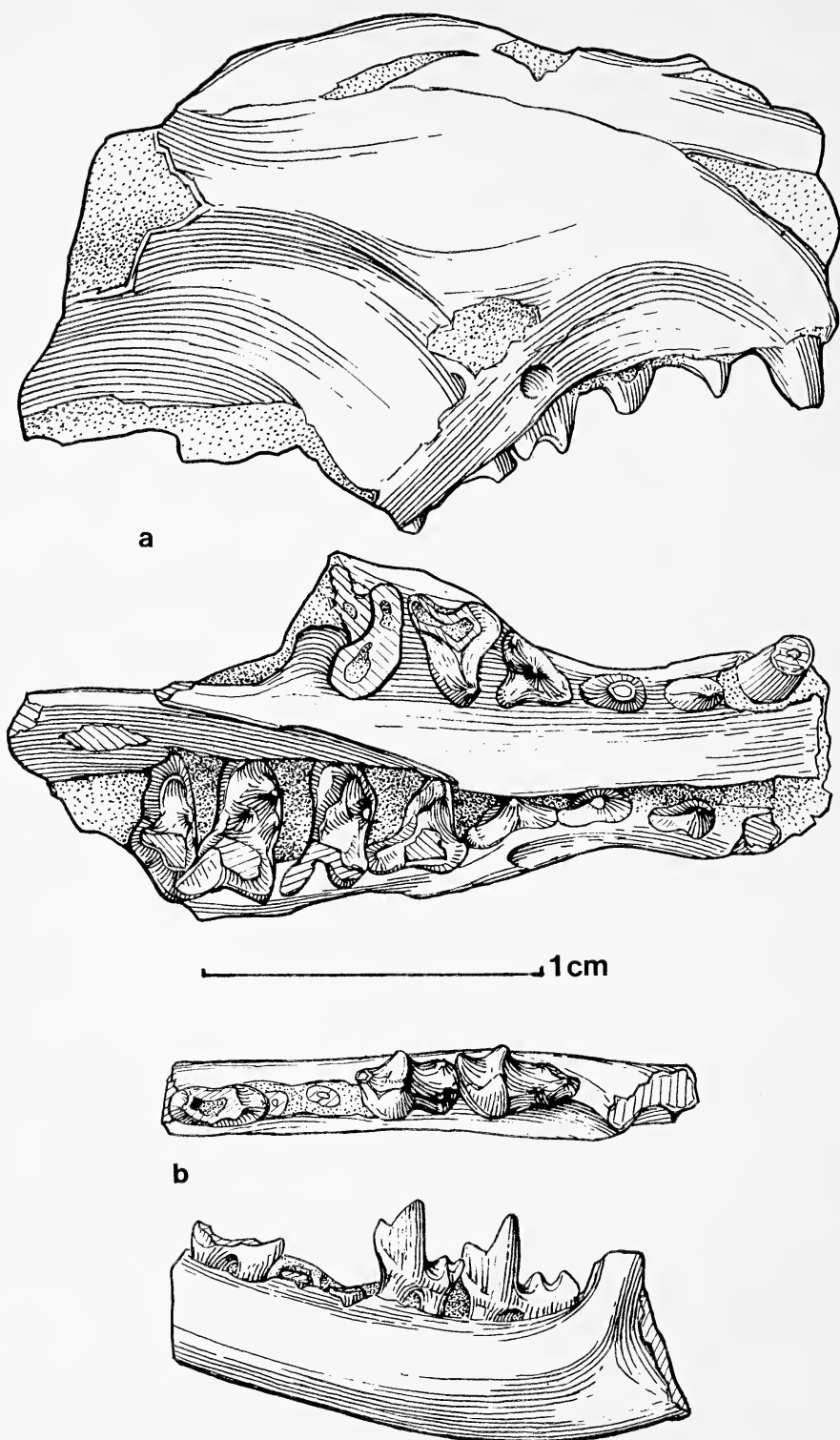


Fig. 5.—*Sinosinopa sinensis* new genus, new species. Holotype, V5677. (a) skull, lateral and palatal views. (b) mandible, crown and lateral views.

Table 1.—Measurements (mm) of *Sinosinopa sinensis* (V5677).

	L	W
C <sup>1</sup>	1.8	1.7
P <sup>1</sup>	1.8	1.0
P <sup>2</sup>	2.2	1.1
P <sup>3</sup>	2.5	2.0
P <sup>4</sup>	3.2	2.8
M <sup>1</sup>	2.7	4.1
M <sup>2</sup>	3.0	4.4
M <sup>3</sup>	1.5	3.9
P <sup>1-4</sup>	10.3	
M <sup>1-3</sup>	7.3	
P <sup>1</sup> -M <sup>3</sup>	16.9	
C <sup>1</sup> -M <sup>3</sup>	20.9	
P <sub>3</sub>	3.0	1.4
P <sub>4</sub>	2.3	
M <sub>2</sub>	3.3	1.9
M <sub>2</sub> trigonid	1.7	1.9
M <sub>2</sub> talonid	1.6	1.7
M <sub>3</sub>	3.7	1.9
M <sub>3</sub> trigonid	1.8	1.9
M <sub>3</sub> talonid	1.9	1.4
Mandibular depth below P <sub>4</sub>	3.4	

Matthew, Granger and Simpson, 1929, as referable to *Sarcodon*, and considered similarities of upper dentitions of *Sarcodon* and *Micropternodus* a result of convergence.

When McKenna et al. (1984) described *Prosarcodon lonanensis*, they made detailed comparisons between *Prosarcodon*, *Sarcodon*, and *Sinosinopa*. *Sinosinopa* differs from *Prosarcodon* and *Sarcodon* in that "it retains all three molars. In *Sinosinopa* both M<sup>1</sup> and M<sup>2</sup> possess a hypocone that juts strongly postero-lingual; in *Prosarcodon* M<sup>2</sup>, the last molar, possesses a narrow cingulum-like hypocone. P<sub>4</sub> of *Sinosinopa* is more elongate than in either *Sarcodon* and *Prosarcodon*." They concluded, "That *Prosarcodon*, *Sarcodon*, and *Sinosinopa* are lipotyphlan insectivores is suggested by the presence of a piriform fenestra in *Prosarcodon*."

There is a well developed hypocone shelf on M<sup>1</sup> of the type specimen of *Sarcodon* (AMNH 20427). *Sarcodon* or *Prosarcodon* could not be ancestral to *Sinosinopa* because *Sinosinopa* has M<sup>3</sup>. Apparently two different lineages of these early insectivores existed in Asia: 1) *Prosarcodon* and *Sarcodon*, which lost M<sup>3</sup> and developed the hypocone shelf; 2) *Sinosinopa*, which kept M<sup>3</sup> but "is more specialized in having jutting hypocones on several upper molars" (McKenna et al., 1984, p. 13).

Order Rodentia Bowdich, 1821  
 Family Paramyidae Miller and Gidley, 1918  
 Subfamily Reithroparamyinae Wood, 1962  
*Asiomys*, new genus

*Type species*.—*Asiomys dawsoni*, new genus, new species; only known species.

*Diagnosis*.—Differs from *Reithroparamys* in having a prominent protoloph on

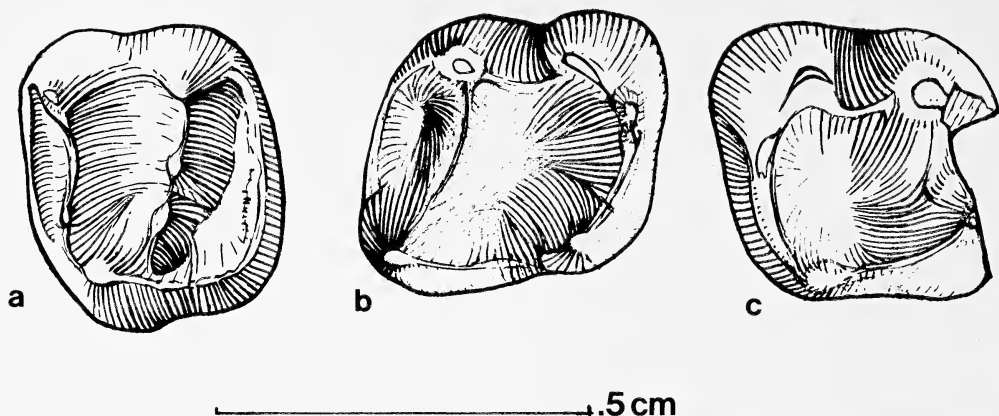


Fig. 6.—*Asiomys dawsoni* new genus, new species. (a) holotype, V5684, M<sup>1</sup>; (b) V5685, M<sub>1</sub>; (c) V5686, M<sub>2</sub>.

M<sup>1</sup>, a closed trigonid basin on M<sub>1</sub>; differs from *Franimys* in having closely approximated paracone and metacone on the upper molars; unlike *Rapamys* M<sub>1</sub> posterior cingulid not close to entoconid.

*Asiomys dawsoni*, new species  
(Fig. 6)

*Holotype*.—V5684, a right M<sup>1</sup> (field no. 77026).

*Referred specimens*.—V5685, right M<sub>1</sub> (field no. 77027); V5686, left M<sub>2</sub>, and incisor (field no. 77028).

*Localities*.—Irdin Manha area (type), Huhe Bulak, and Daatein Obo.

*Diagnosis*.—Medium-sized reithroparamyine; upper and lower cheek teeth nearly square in crown view; double metaconules on upper molar; protocone-metaconules-metacone forming a crest; ectolophid developed on lower molar.

*Description*.—M<sup>1</sup> (L, 3.8; W, 4.6): protocone prominent, paracone and metacone conical, close together; paraconule near protocone, paracone-paraconule-protocone forming paraloph; double metaconules, that near protocone larger in size, the other not prominent; metaloph connected with protocone directly, not with hypocone; mesostyle relatively apparent; hypocone prominent; hypocone shelf relatively broad; posterior cingulum low and wide but not enclosing metacone; anterior cingulum narrow and short, ended at the paraconule lingually; straight valley on lingual wall between protocone and hypocone but not reaching base. M<sub>1</sub> (L, 4.0; W, 3.9): double crests from protoconid forming an anterior-posterior short, closed trigonid basin; ectolophid developed but not closed to labial side and connecting protoconid and hypoconid; hypoconid relatively prominent, connecting with posterior cingulum; two small points on posterior cingulum; entoconid isolated. M<sub>2</sub> (W, 4.0): similar to M<sub>1</sub>, but larger in size and protolophid II shorter, so trigonid basin opens posteriorly.

*Discussion*.—The discovery of middle Eocene *Asiomys dawsoni* is the first record of the Reithroparamyinae in Asia. This subfamily includes three other genera, *Reithroparamys*, *Franimys*, and *Rapamys*, all from North America (Wood, 1962).

In size, *Asiomys* is close to both paramyines and reithroparamyines. The upper molars of the paramyines have only one metaconule, while the reithroparamyines have double metaconules. The earlier members of the Reithroparamyinae, such as *Reithroparamys*, have double metaconules on the upper molars, one larger and another smaller. In addition to this similarity, the referred lower teeth from Inner Mongolia resemble reithroparamyines in features such as medium size and entoconid completely separate from posterior cingulum.

Table 2.—Measurements (mm) of *Tamquammys wilsoni*.

	V5678		V5679			V5680		
	L	W	L	W trigonid	W talonid	L	W trigonid	W talonid
dP <sup>3</sup>	0.7	0.9						
dP <sup>4</sup>	1.2	1.7						
P <sup>4</sup>	1.3	1.7						
M <sup>1</sup>	1.4	1.8						
M <sup>2</sup>	1.5							
Diastema	4.0							
P <sub>4</sub>			1.5	1.1	0.9			
M <sub>1</sub>			1.5	1.3	1.5	1.3	1.2	1.4
M <sub>2</sub>			1.7	1.5	1.6	1.7	1.4	1.5
M <sub>3</sub>			1.9	1.6	1.5	1.8	1.5	1.4
P <sub>4</sub> –M <sub>3</sub>			6.7					
M <sub>1</sub> –M <sub>3</sub>			5.1			4.5		

M<sup>1</sup> of the Inner Mongolian species differs from that of *Reithroparamys* in several points. The protoloph of the Inner Mongolian specimen is more prominent, whereas it is indistinct, if present at all, in *Reithroparamys*. In *Reithroparamys delicatissimus*, for instance, the end of the protoloph is anterior to the protocone, not connected with it. The protolophid II of *Reithroparamys* is short, not connecting with the metaconid to form a closed trigonid basin. The Inner Mongolian species has a well developed ectolophid, whereas some reithroparamyines, such as *R. debequensis* and *R. pattersoni*, have only a mesoconid or nothing.

The main distinctive characters of *Franimys* occur in its skull and limbs, but the genus is characterized also by having paracone and metacone of its upper molars well separated. This character is quite different from the condition in the Inner Mongolian species. Besides this, *Franimys* has a very short protolophid II.

M<sup>1</sup> and M<sup>2</sup> of *Rapamys* have two or three metaconules. Another of its main characters never appeared on other reithroparamyines—having a prominent but short posterior cingulid that is very close to the entoconid.

Family Cocomyidae Dawson, Li and Qi, 1984  
*Tamquammys* Shevyreva, 1971  
*Tamquammys wilsoni* Dawson, Li and Qi, 1984  
(Figs. 7, 8; Table 2)

*Holotype*.—V5678, anterior portion of skull with broken incisors, right P<sup>4</sup>, left dP<sup>3</sup>–M<sup>2</sup>.

*Referred specimens*.—V5679, right jaw with I, P<sub>4</sub>–M<sub>3</sub>; V5680, right jaw with M<sub>1–3</sub>; V5681, M<sub>1</sub>; V5682, M<sub>2</sub> (broken); V5683, left lower molar. All specimens came from one nodule.

*Locality*.—Huhe Bulak.

*Discussion*.—Discoveries in recent years have led to clarification of the classification of Ctenodactyloidea (Dawson et al., 1984). Only one family, Ctenodactylidae, was recognized when Simpson (1945) established the superfamily Ctenodactyloidea. Now, two other ctenodactyloid families, Cocomyidae and Yuomyidae, have been established.

Distribution of *Tamquammys* is middle Eocene in Kazakhstan and Inner Mongolia. Revised diagnosis of *Tamquammys* is as follows (Dawson et al., 1984, pp.

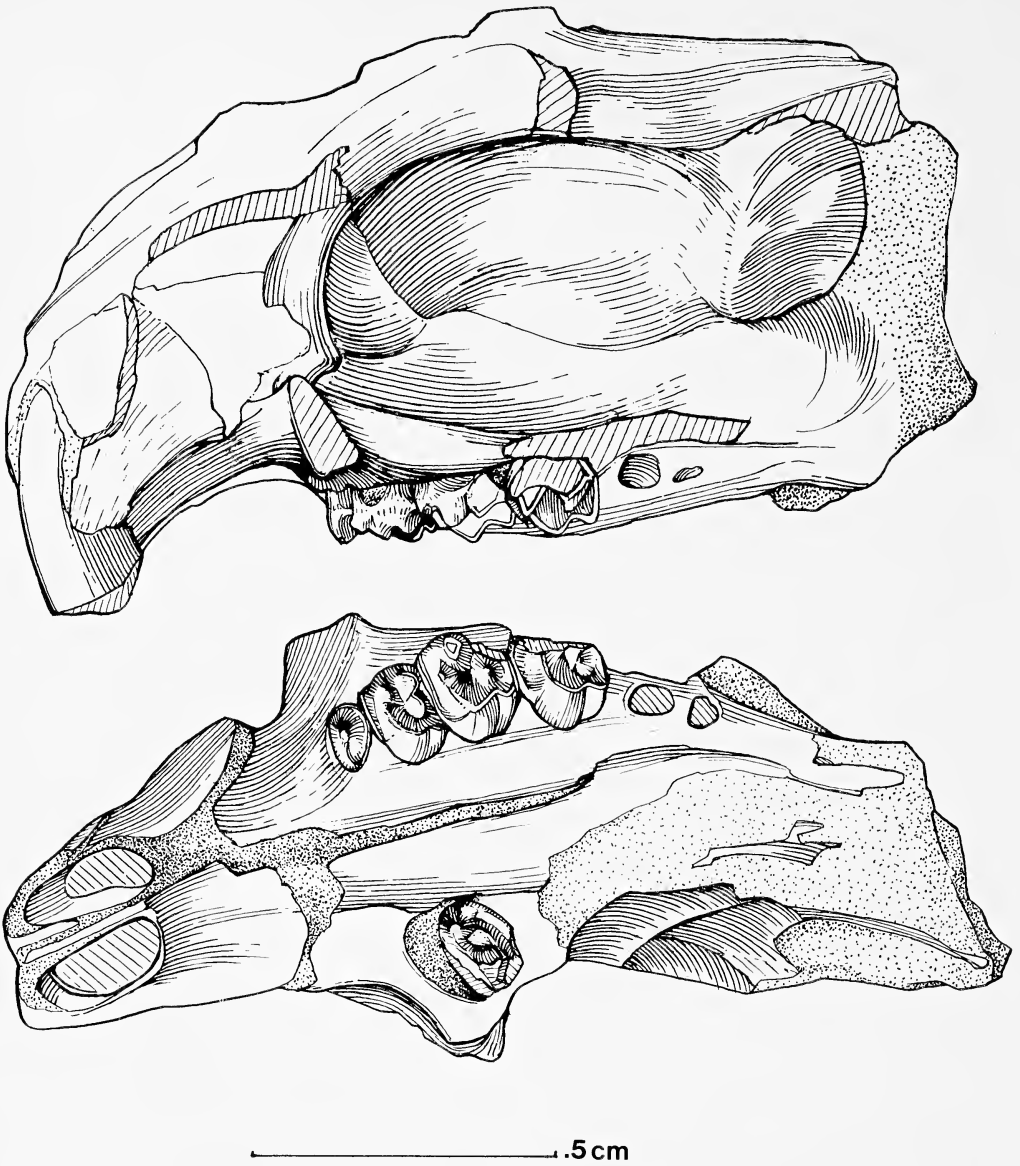


Fig. 7.—*Tamquammys wilsoni*. Holotype, V5678, skull, left lateral and palatal views.

142–143): “Ctenodactyloid rodent with skull hystricomorphus, lower jaw sciurognathous. Cheek teeth increase in size from front to back, have well developed conules in upper teeth, well developed lophs in lowers.  $P^4$  with single buccal cusp.  $P_4$  with relatively short and narrow talonid.” *Tamquammys wilsoni* has the following diagnosis: “Smaller than *T. tantillus*;  $P_4$  has talonid less well developed posterobuccally, hypoconid-hypoconulid ridge more oblique, less transverse in orientation.”

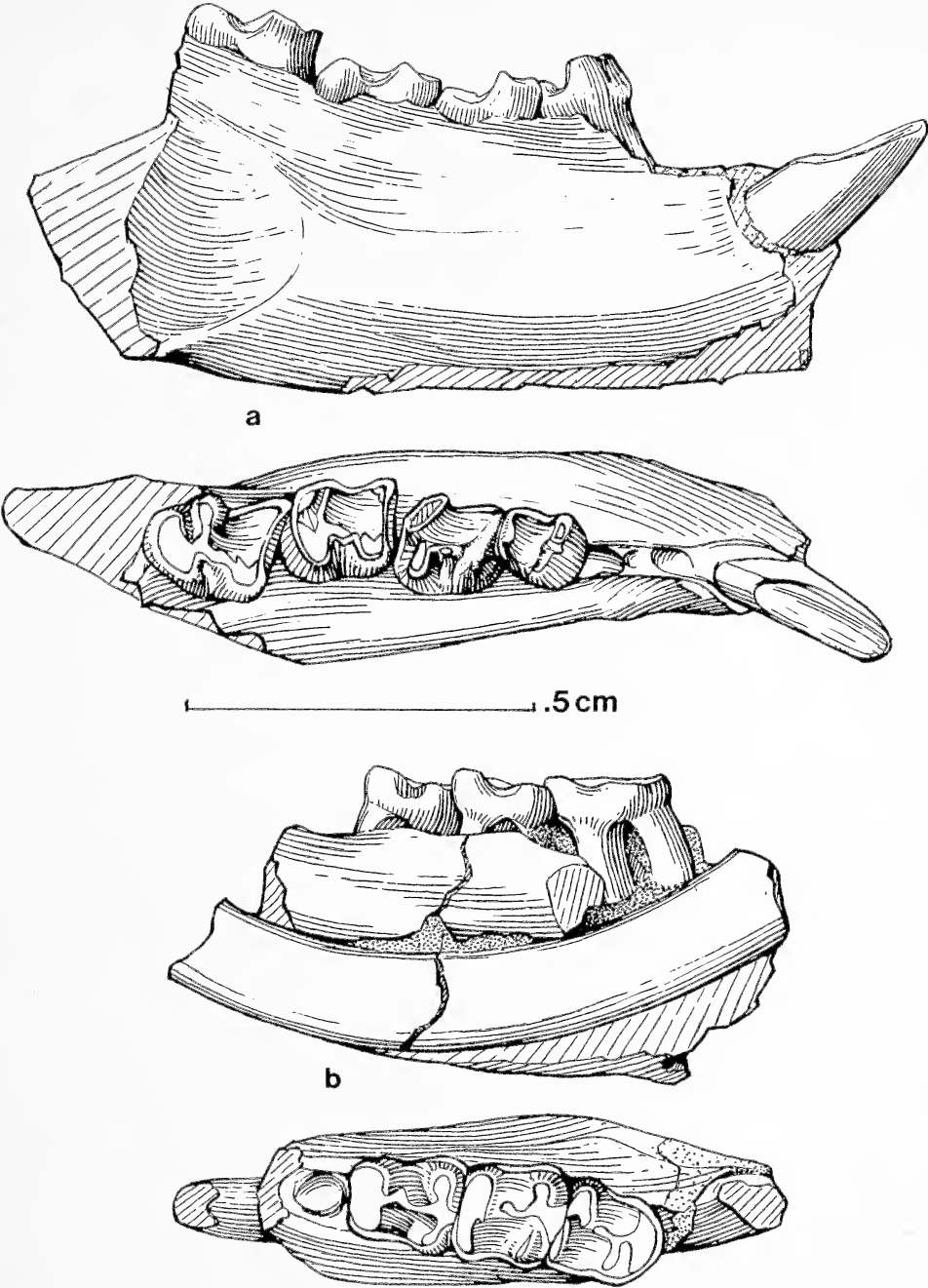


Fig. 8.—*Tamquammys wilsoni*. (a) V5680, lateral and crown views; (b) V5681, medial and crown views.

Order Acreodi Matthew, 1909  
Mesonychidae Cope, 1875  
*Mongolonyx* Szalay and Gould, 1966  
*Mongolonyx dolichognathus* Szalay and Gould, 1966  
(Fig. 9)

*Holotype*.—AMNH 26661, lower jaw with several well-preserved teeth, coronoïd processes broken off; collected during the 1930 Central Asiatic Expedition; AMNH field no. 895.

*Referred specimens*.—AMNH 26662 (AMNH field number 907), a complete left maxilla with P<sup>2</sup>–M<sup>2</sup>. Newly referred specimens V5690, M<sup>2</sup> (field number 77039); V5691, M<sub>2</sub> (field number 77031).

*Localities*.—7 miles west of Camp Margetts (type), Huhe Bulak, Bayan Ulan.

*Discussion*.—When Szalay and Gould (1966) described this species, they mentioned the uniqueness of M<sup>2</sup>: “The last molar, M<sup>2</sup>, is the best preserved and most diagnostic tooth in the maxilla. The paracone is at least twice the size of the protocone, while the small metacone is connate with the posterior wall of the paracone. M<sup>2</sup> is only about two-thirds as wide as the preceding M<sup>1</sup>.”

Newly discovered specimens from Inner Mongolia are two teeth: M<sup>2</sup> (V5690) and M<sub>2</sub> (V5691). Characters of M<sup>2</sup> are: 1) paracone twice the size of protocone; 2) metacone very small; 3) labial tooth wall convex; and 4) cingula very weak. M<sub>2</sub> has a prominent paraconid (although broken), a very strong protoconid, a relatively weak hypoconid. The enamel ridge at the base of the tooth is almost a straight line. M<sup>2</sup> (V5690) is quite similar to that of AMNH 26662 in both size and morphology, and M<sub>2</sub> (V5691) is close also to M<sub>2</sub> of the type specimen. Discovery of these two teeth establishes the geological provenance of *Mongolonyx dolichognathus* as the Arshanto beds.

*Measurements*.—L/W: M<sup>2</sup> (V5690) 26.3/27.2 mm, (AMNH 26661) 26.8/27.9 mm; M<sub>2</sub> (V5691) 31.2/16.5 mm; (AMNH 26662) 32(?) /16.5.

*Mesonyx* Cope, 1872  
*Mesonyx* sp. cf. *M. obtusidens* (Cope, 1872)  
(Figs. 10, 11; Table 3)

*Referred specimens*.—V5692: left P<sup>4</sup>, with three roots (field no. 77036-2); V5696.1, M<sup>2</sup> (field no. 77027); V5693: M<sup>2</sup>, with three roots (field no. 77036-2); V5694: lower canine (field no. 77027); V5695, 1–2: P<sub>3</sub> or P<sub>4</sub> (field no. 77027); and V5696: M<sub>3</sub> (field no. 77026).

*Localities*.—Huhe Bulak and Irdin Manha area.

*Description*.—P<sup>4</sup>: paracone larger than protocone; parastyle prominent; metastyle very weak. M<sup>2</sup>: protocone slightly larger than paracone, two convex crests on labial wall of protocone, protocone wall flat between the two crests; parastyle smaller in size; metacone larger; parastyle and metacone oblique; metastyle low but clear; extremely worn cingulum on buccal wall, clearer near metastyle; anterior edge of tooth concave, whereas posterior edge is relatively straight.

P<sub>3</sub> (or P<sub>4</sub>): paraconid small cusp; protoconid large, relatively far back; position of hypoconid much lower than that of protoconid; no cingulum. M<sub>3</sub>: crown narrow and low; paraconid relatively prominent; protoconid larger; length of hypoconid two-thirds length of whole tooth.

*Discussion*.—Cope (1872) first reported *Mesonyx obtusidens*, but the most complete skull (AMNH 12643) with upper cheek teeth was described by Matthew (1907). According to the descriptions of Matthew, M<sup>1</sup> of this species has a metastyle. Morphologically, the Inner Mongolian specimen is quite similar to AMNH 12643 at least in crown view. However, the Inner Mongolian specimen is larger



Table 3.—Measurements (mm) of *Mesonyx* sp. cf. *M. obtusidens*.

	L	W	L	W
P <sup>4</sup> (V5692)	15.6	14.8		
M <sup>2</sup> (V5693; V5696.1)	19.7	18.3	20.0	17.5
P <sub>3</sub> (V5695-1)	19.2	8.5		
P <sub>4</sub> (V5695-2)	19.7	9.8		
M <sub>3</sub> (V5696)	16.9	7.3		

and the parastyle and metacone are oblique, whereas those of AMNH 12643 are almost erect. The M<sub>3</sub> found at locality 77026 is unusual and is only tentatively referred to this species.

V5696.1, an M<sup>2</sup>, is similar to V5693 (M<sup>2</sup>), except for the absence of a metastyle and being longer (L, 20.0 mm; W, 17.5 mm).

*Hapalodectes* Matthew, 1909  
*Hapalodectes?* *serus* (Matthew and Granger, 1925)  
(Fig. 12)

*Referred specimen.*—V7316, a broken lower jaw with posterior part of M<sub>2</sub> and single root of M<sub>3</sub> (field no. 77027).

*Locality.*—Huhe Bulak.

*Discussion.*—Matthew and Granger (1925*b*) described two mesonychids, *Hapalodectes serus* (only one tooth) and *H. auctus*, the former being smaller than the latter. M<sub>2</sub> of V7316, which is broken anteriorly, resembles that of *Hapalodectes serus*: it is hypsodont and the crest of the posterior part is sharp. There is a shallow masseteric fossa on the lower jaw.

*Measurements.*—AMNH 20172 (lower cheek tooth): 5.6 mm; V7316: 5.3 mm (ca.).

Order Pantodonta Cope, 1873  
Family Coryphodontidae Marsh, 1876  
*Metacoryphodon*, new genus

*Type species.*—*Metacoryphodon luminis* new genus, new species.

*Diagnosis.*—Larger than *Coryphodon*; unlike *Eudinoceras*, P<sup>2-3</sup> protocristae present, canine more robust and longer.

*Metacoryphodon luminis*, new species  
(Fig. 13; Table 4)

*Holotype.*—V5697, a broken skull with canines (not complete), right P<sup>1</sup>–M<sup>3</sup> and left P<sup>2</sup>–M<sup>3</sup> (field no. 1P<sub>5</sub>H<sub>8</sub>).

*Locality.*—Ulan Bulak.

*Diagnosis.*—Canine extremely robust; P<sup>2</sup> and P<sup>3</sup> with apparent pre-protocristae; post-protocristae tend to disappear; M<sup>3</sup> has trace of paracone, ectolophs very long on the molars.

*Description.*—Nasal bone (broken) wide transversely, postcanine diastema not long; frontal bone wide and flat; zygomatic arch very strong. C<sup>1</sup>: very robust; transverse section round; the growing directions of the two canines not upright, but inclined outward. P<sup>1</sup>: no protocone; paraloph longer than metaloph; cingulum developed. P<sup>2</sup>: protocone strong with apparent pre-protocrista and weak post-protocrista; pre-protocrista extends downward and becomes a part of anterior cingulum, but not connected to inner cingulum; paraloph and metaloph very long, the two joining to form a “V”; parastyle more swollen than metastyle. P<sup>3</sup>: pre-protocrista and post-protocrista are developed but weak; parastyle

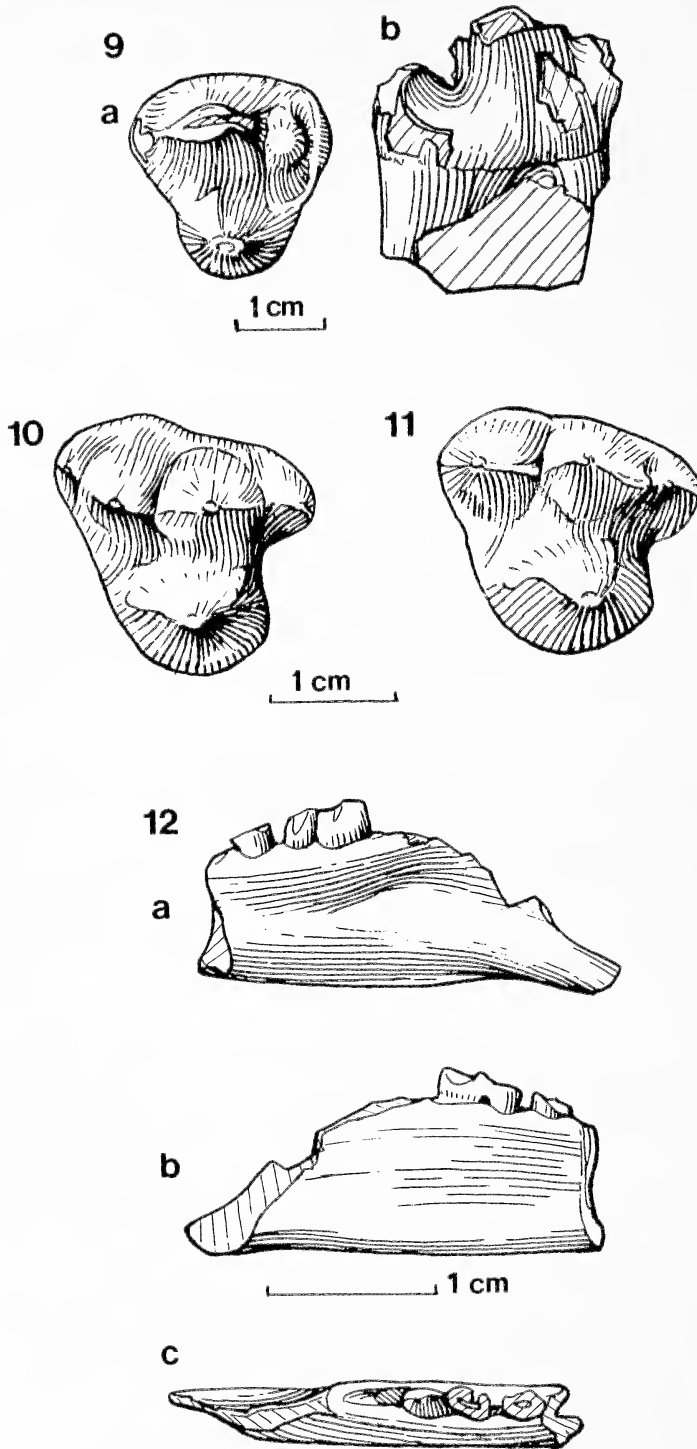


Fig. 9.—*Mongolonyx dolichognathus*. (a) V5690, left M<sup>2</sup>; (b) V5691, M<sub>2</sub>.

Fig. 10, 11.—*Mesonyx* sp. cf. *M. obtusidens*. 10. V5693, right M<sup>2</sup>. 11. V5696.1, right M<sup>2</sup>.

Fig. 12.—*Hapalodectes? serus*. V7316, lower jaw. (a) external, (b) internal, (c) crown view.

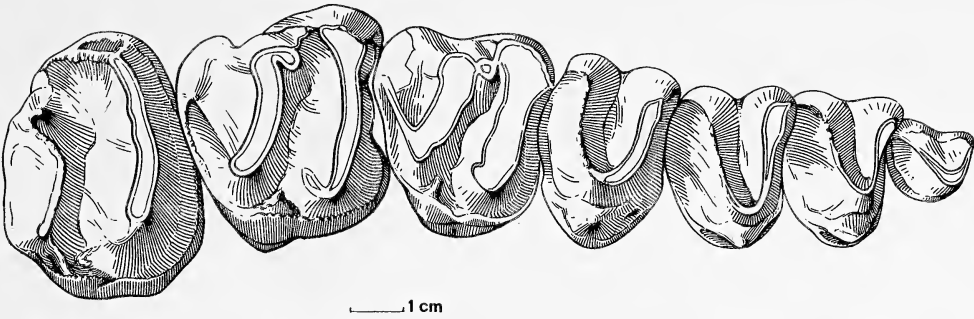


Fig. 13.—*Metacoryphodon luminis* new genus, new species. Holotype, V5697, right P<sup>1</sup>–M<sup>3</sup>, crown view.

close to metastyle, so the valley between paraloph and metaloph is narrow. P<sup>4</sup>: pre-protocrista very weak; some crenulations on the anterior cingulum; post-protocrista weak, so protocone almost isolated. M<sup>1</sup>: protocone high; protoloph almost parallel with ectoloph; parastyle relatively prominent; hypocone small, but distinct; metastyle swollen; cingulum present on anterior, inner, and posterior sides of crown, but not buccally. M<sup>2</sup>: quite similar to M<sup>1</sup>; ectoloph long; hypocone relatively large. M<sup>3</sup>: wider but shorter than M<sup>2</sup>; protoloph very long, with trace of paraconule; parastyle low; paracone isolated; ectoloph short, its central part convex anteriorly; no metastyle.

*Discussion.*—Some characters of this species are intermediate between *Coryphodon* and *Eudinoceras*. The type specimen was found in 1977 by the staff of the Inner Mongolian Geological Mapping Team. In size it is close to *Eudinoceras mongoliensis* but larger than *Coryphodon*.

*Eudinoceras mongoliensis* (P<sup>3</sup> or P<sup>4</sup>) was first described from Irдин Manha beds by Osborn (1924). In 1931, Osborn and Granger described another species, *E. kholobolchiensis*, from Kholobolchi Nor Basin, Mongolian People’s Republic and, in 1932, described ?*Eudinoceras mongoliensis* from a lower jaw with cheek teeth. Many years later, Tong and Tang (1977) reported a new species, *Eudinoceras crassum*. During the summer field season of 1975, the author and the staff of Geological Mapping Team of Inner Mongolia discovered a broken skull and lower jaw of *Eudinoceras mongoliensis* with upper and lower incisors, canines, and cheek teeth on one side.

Although there are some differences between *E. mongoliensis* and *E. kholobolchiensis*, protocones of P<sup>2</sup> and P<sup>3</sup> in both are isolated, that is, there are no pre-protocristae and post-protocristae. *Metacoryphodon luminis* has apparent pre-

Table 4.—*Measurements (mm) of Metacoryphodon luminis (V5697).*

	L	W
C <sup>1</sup>	37.0	41.0
P <sup>1</sup>	19.0	17.0
P <sup>2</sup>	25.5	34.8
P <sup>3</sup>	27.0	37.9
P <sup>4</sup>	27.4	43.7
M <sup>1</sup>	38.0	43.6
M <sup>2</sup>	46.5	52.4
M <sup>3</sup>	44.4	57.1
P <sup>1</sup> –4	96.0	
M <sup>1</sup> –3	122.7	
P <sup>1</sup> –M <sup>3</sup>	216.6	

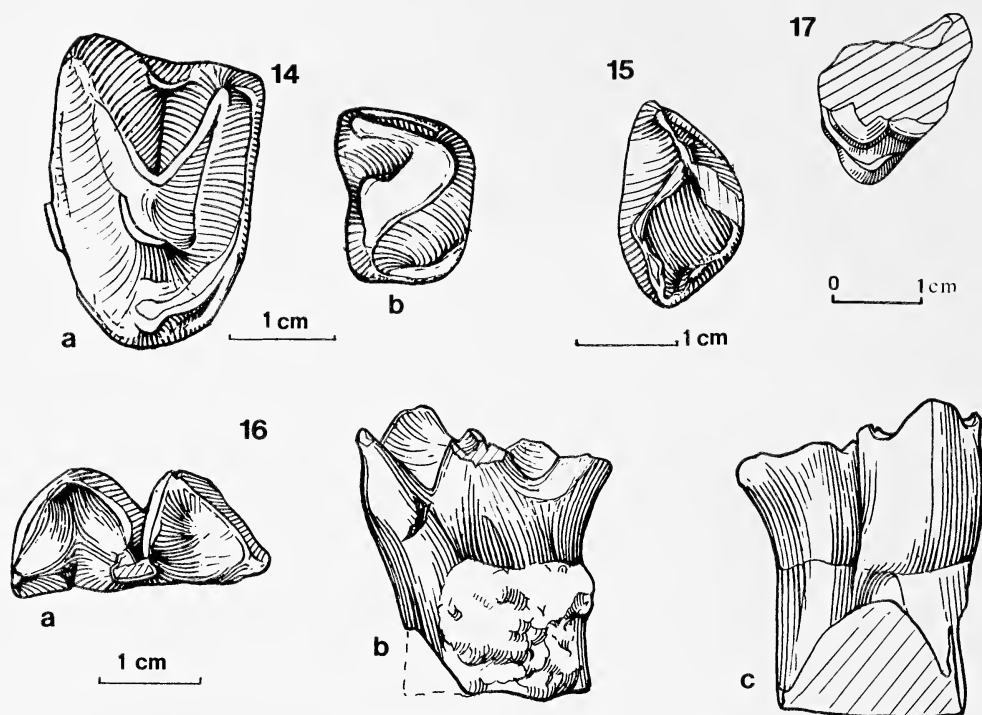


Fig. 14.—*Metacoryphodon?* *minor* new species. (a) Holotype, V5698, P<sup>2</sup>; (b) V5699, P<sub>2</sub>.

Fig. 15.—*Metacoryphodon* sp. V5700, right P<sub>1</sub>.

Fig. 16.—*Pantolambdodon fortis*. V5687, right M<sub>1</sub>. (a) crown, (b) internal, (c) external views.

Fig. 17.—*Pantolambdodon?* *minor*. V5701, broken right M<sup>1</sup>.

protocristae and weak post-protocristae on P<sup>2</sup> and P<sup>3</sup>. The canine of *E. mongoliensis* is inclined laterally and its crown is sword-shaped with saw-like edges, whereas the canine of *M. luminis* is more robust and longer and is directed anteriorly, as are the lower canines of *?Eudinoceras mongoliensis*.

*Coryphodon* is somewhat smaller than *Metacoryphodon*. P<sup>1-4</sup> of *Coryphodon* have apparent pre-protocristae and post-protocristae.

*Metacoryphodon* is morphologically an evolutionary intermediate between early Eocene *Coryphodon* and the late middle Eocene *Eudinoceras* and *Hypercoryphodon*. In the evolution from *Coryphodon* to *Metacoryphodon* to *Eudinoceras* the pre-protocristae and post-protocristae gradually disappeared.

***Metacoryphodon?* *minor*, new species**  
(Fig. 14)

*Holotype*.—V5698, a right P<sup>2</sup> (field no. 77027).

*Referred specimen*.—V5699, a right P<sub>2</sub> (field no. 77039).

*Locality*.—Huhe Bulak.

*Diagnosis*.—Smaller than *M. luminis*; metastyle of P<sup>2</sup> more prominent than parastyle; opening of V-shaped valley formed by paraloph and metaloph is blocked by cingulum; pre-protocristae well developed, no post-protocristae; P<sub>2</sub> lacking outer and inner cingula.

Table 5.—Measurements (mm) of *Pantolambdodon inernis* and *P. fortis*.

	<i>Pantolambdodon inernis</i>						<i>Pantolambdodon fortis</i>			
	AMNH 21558		AMNH 22100		AMNH 21748		AMNH 26127		V5687	
	L	W	L	W	L	W	L	W	L	W
M <sub>1</sub>	20.0	9.5	20.0	11.0			29.0	13.0	27.8	14.5
M <sub>2</sub>	21.5	11.0	22.7	11.5						
M <sub>3</sub>			26.0	11.5	23.0	9.0				
M <sub>1</sub> trigonid	11.5	9.0	11.0	10.0			16.0	13.5	14.0	14.0
M <sub>1</sub> talonid	8.5	9.0	9.0	10.0			16.0	13.0	14.0	12.5
M <sub>2</sub> trigonid	11.5	9.5	13.0	10.5						
M <sub>2</sub> talonid	10.0	9.0	9.5	9.5						
M <sub>3</sub> trigonid			15.0	11.0	12.5	9.5				
M <sub>3</sub> talonid			11.0	8.0	11.0	7.0				

*Discussion.*—Both teeth are small. P<sub>2</sub> has well developed pre-protocristae, but no trace of post-protocristae. This character is quite different in *M. luminis*. The protocone of *M.?* *minor* is not as strong as that of *M. luminis*, its parastyle is relatively weaker, and there are no traces of a parastyle or metastyle. In addition, the opening of the V-shaped valley in *M. luminis* is not blocked by the cingulum.

Because no lower jaw of *M. luminis* is known, comparison with P<sub>2</sub> (V5699) is not possible. P<sub>2</sub> of *Metacoryphodon?* *minor* (L, 18.3 mm; W, 14.6 mm) is smaller than that of *Eudinoceras mongoliensis*, and following the size of P<sub>2</sub> (L, 22.3 mm; W, 32.2 mm), is certainly smaller than *M. luminis*.

*Metacoryphodon* sp.  
(Fig. 15)

*Referred specimen.*—V5700, a right P<sub>1</sub> (field no. 77036H2).

*Locality.*—Huhe Bulak.

*Discussion.*—This tooth was found at a lower level. The size of P<sub>1</sub> is close to that of *Eudinoceras mongoliensis* but it shows several differences from that taxon: 1) paralophid of P<sub>1</sub> of *E. mongoliensis* is shorter and has a small cusp on the anterior end, whereas the paralophid of V5700 is longer and has two small cusps (one on the anterior end and another one at the middle of paralophid); 2) the paralophid and metalophid of *E. mongoliensis* are almost on a straight line, whereas the same lophids of V5700 form a V with a large opening; 3) V5700 has a cingulum behind the metastylid and a small cusp (worn) on the posterior end of the metastylid, whereas these are absent in *Eudinoceras mongoliensis*; 4) V5700 has no cingulum, but P<sub>1</sub> of *E. mongoliensis* is enclosed by cingulum at the base of the crown.

*Measurements.*—P<sub>1</sub> (V5700), L: 22.1 mm, W: 13.1 mm.

Family Pantolambdodontidae Granger and Gregory, 1934

*Pantolambdodon* Granger and Gregory, 1934

*Pantolambdodon fortis* Granger and Gregory, 1934

(Fig. 16; Table 5)

*Holotype.*—AMNH 26127, fragmentary right ramus of lower jaw with M<sub>1</sub> and alveoli of all anterior teeth.

*Referred specimen.*—V5687, a right M<sub>1</sub> (field no. 77027).

*Localities.*—8 miles north of Tukhum Lamasery; Huhe Bulak.

*Discussion.*—The first fossils of this taxon were found in 1925 and 1928, and

the systematic position of this family was reached by roundabout means. When Granger and Gregory (1934) studied these materials, they first decided that they "are dealing with a placental mammal of some sort from the fact that the dental formula:  $I_3, C_1, P_4, M_3$ , is the classic primitive eutherian formula." They made many comparisons between the Mongolian types and many kinds of mammals, such as some South American mammals, chalicotheres, titanotheres, artiodactyls, condylarths, and dinoceratans.

At last, Granger and Gregory (1934, pp. 5–6) discovered that these Mongolian types are related to pantodonts: "When we come to *Pantolambda* and *Titanoides*, however, we find some apparently reliable indications of remote relationship to the Mongolian types, especially in the form of the premolars and molars. In spite of the fact that *Titanoides* is a graviportal form almost as big as *Coryphodon*, it shares the following features with the Mongolian fossils: (1) Dental formula of primitive placental type; (2)  $P_1, P_2$  compressed; (3) talonid fossa of premolars formed between the posterior ridge connected with the main cone and a transverse metaconid ridge; (4) molar talonids with V-shaped crests; (5) talonid of  $M_3$  narrower than trigonid; (6)  $M_3$  with reduced or no hypoconulids; (7)  $M_1, M_2$  with no trace of hypoconulid; (8) molars not crowded but slightly spaced; (9) coronoid process inclined backward. *Titanoides* is distinguished from the Mongolian forms by its relatively gigantic size, powerful, more erect incisors and canines; relatively shorter, more massive jaw, etc.

"From *Pantolambda* the present form differs in its much more elongate slender jaw, somewhat procumbent front teeth, more hypsodont cheek teeth, compressed premolars; the molars have much larger anterior V's and smaller posterior V's; the ascending ramus sloped backward and is distinctly delicate."

Ye (1983) referred to this family several teeth collected in Ulan Shireh, which was the type locality of this genus. A broken maxilla with upper cheek teeth was found in Aliusu. These cheek teeth, now under study, belong to a species of this genus.

*Pantolambdodon* has two species, *P. inermis*, and *P. fortis*. The main differences between the two species are in size, the former smaller, the latter larger. The newly discovered specimen (V5687) is similar to *P. fortis* in both size and morphology. The tooth has a shallow valley anterior to the crista obliqua, which has never been seen on other specimens.

***Pantolambdodon? minor*, new species**  
(Fig. 17)

*Holotype*.—V5701, a broken  $M^1$  (field no. 77026; L, protocone to parastyle, 21.0 mm).

*Referred specimen*.—V6706, a left  $M_1$  (*Pantolambdodon inermis* of Ye, 1983; L/W of trigonid, 15/6.5 mm).

*Localities*.—Irdin Manha area, Ulan Shireh area.

*Diagnosis*.—Small size, pre-protocrista short; post-protocrista long; distance between paracone and metacone short, having a small metastylid on  $M_1$ .

*Description*.— $M^1$ : protocone strong; pre-protocrista short, extending down anteriorly; post-protocrista long, extending down posteriorly; paracone and metacone relatively robust; distance between paracone and parastyle relatively long; mesostyle preserved only as a small piece of crest.  $M_1$ : angle of V-shaped crest is  $55^\circ$ , metastylid apparent, smaller in size (Ye, 1983).

*Discussion*.—The two teeth were found at different localities: V5701 from Arshanto beds in the Irdin Manha area; V6706 from Ulan Shireh (beds). Although

V5701 ( $M^1$ ) is broken on the buccal side, the diagnostic part is well preserved, allowing comparison between this  $M^1$  and an undescribed specimen from Aliusu (see *P. fortis* above). The distance between protocone and parastyle is two-thirds that in the Aliusu specimen, while the distance between protocone and the base of mesostyle is only half that in the Aliusu specimen. However, the two specimens share some features: protocone very well developed; pre-protocrista and post-protocrista similar; paracone close to metacone; and roots underneath paracone-parastyle equally robust.

Order Dinocerata Marsh, 1873

Family Uintatheriidae Flower, 1876

*Gobiatherium* Osborn and Granger, 1932

*Gobiatherium mirificum* Osborn and Granger, 1932

(Figs. 18, 19, 20a–c, 21, 22; Table 6)

*Holotype*.—AMNH 26624, a complete and nearly perfect skull.

*Paratype*.—AMNH 26630, a nearly complete pair of lower jaws, lacking the incisors.

*Referred specimens*.—V5702: broken right maxilla, with  $P^{3-4}$ ,  $M^{2-3}$  and left  $M^1$  (field no. 77036-2); V5703: broken  $P^4$  (77034); V5704: right lower jaw with  $P_2$ – $M_3$  (77036-2); V5705: broken lower jaw with right  $P_2$ – $M_3$  ( $M_2$  and  $M_3$  heavily broken) and left  $P_{3-4}$  (field number 1P<sub>5</sub>H<sub>8</sub>); V5706: left  $M_3$  (77036-2); V5707: right  $M_3$  (77036-2); V5708: posterior part of left  $M_3$  (77036-2); V5709: incisor (77021); V5710: lower jaw of a juvenile with  $dP_2$ – $M_1$  (77036-2).

*Localities*.—25 miles southwest from Iren Dabasu; Huhe Bulak; Arshanto Obo.

*Description*.— $P^3$ : in crown view nearly quadrangular, paraloph and metaloph forming “V”; paraloph somewhat convex anteriorly; paracone very prominent, its apex pointing posterolingually; a lingual cuspule, the paraconule, near the paracone; metaloph straight; metaconule relatively prominent; anterior and posterior cingula very wide, connecting at base of protocone and inclined somewhat upward; external cingulum very weak.  $P^4$ : paraloph more convex anteriorly; paracone prominent, but smaller than on  $P^3$ ; rib-like crest on posterolingual side of paracone; metaloph straight; relatively prominent metaconule forming rib-like crest; anterior and posterior cingula very well developed; no external cingulum;  $P^{3-4}$  retain some trace of cement.  $M^1$ : paraloph straight; paraconule and metaconule present; metaloph relatively straight; anterior and posterior cingula narrower than on  $P^{3-4}$  or  $M^{2-3}$ ; weak external cingulum.  $M^2$ : paraloph relatively straight; paracone somewhat swollen; metaloph straight; metaconule present; cusp, possibly hypocone, on central part of posterior wall of protocone; anterior cingulum gradually widened from labial to lingual side; posterior cingulum also wide; anterior and posterior cingula separated at base of protocone; no external cingulum.  $M^3$ : largest of upper cheek teeth; paracone swollen; paraconule present; distinct, saddle-like pit between paraconule and protocone; metacone prominent; metaconule present (although broken); anterior cingulum wide; posterior cingulum probably wide (also broken).  $I_1$  (more than half preserved) characteristically notched.  $P_2$ : smallest of lower cheek teeth; protoconid high; paraconid low; protoconid-metaconid-hypoconid forming a crest; hypoconulid forming posterior cingulum; with trace of cement.  $P_3$ : paraconid very small; metaconid high; protoloph straight; mesoconid large and low; cingulum lying anterior to paracone on lingual side; hypoconulid forming posterior cingulum; trace of cement behind hypoconid.  $P_4$ : larger in size but otherwise similar to  $P_3$ .  $M_1$ : paraconid prominent; vertical crest of hypoconulid faint; distance between posterior cingulum and transverse crest (both formed by hypoconulid) is long, forming a wide posterior shelf.  $M_2$ : (V5706) metaconid high; mesoconid prominent; paraconid distinct; hypoconulid forming posterior cingulum; entoconid very prominent.  $M_3$ : (V5705) largest tooth; protoconid and paraconid distinct, joined by low crest; metaconid high; mesoconid prominent; hypoconid parallels hypoconulid; entoconid somewhat swollen and forming rib-like crest.

Juvenile (V5710): body of lower jaw rather slender; ascending ramus wide anteroposteriorly; masseteric fossa shallow; short  $dP_1$ – $dP_2$  diastema.  $dP_2$ : rather long anteroposteriorly; paraconid and mesoconid distinct; protoconid very high; metaconid relatively prominent; mesoconid clear; hypoconid forming a transverse crest and connected to mesoconid; hypoconulid forming posterior cingulum.  $dP_3$ : crown view quadrangular; paraconid relatively prominent; anterior cingulum extremely weak; hy-

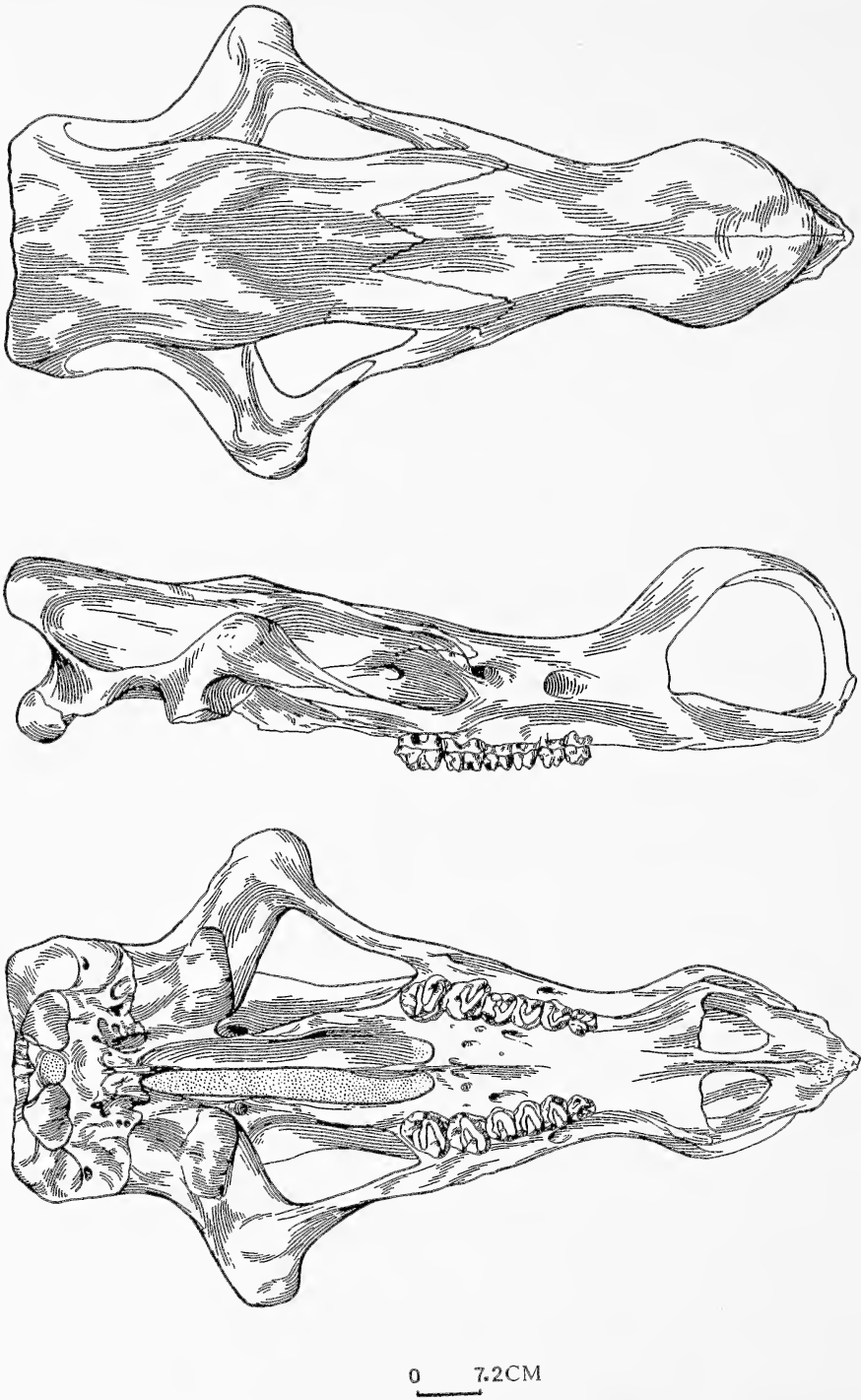


Fig. 18.—*Gobiatherium mirificum*. Holotype, AMNH 26624, dorsal, lateral, and palatal views of skull (from Osborn and Granger, 1932).



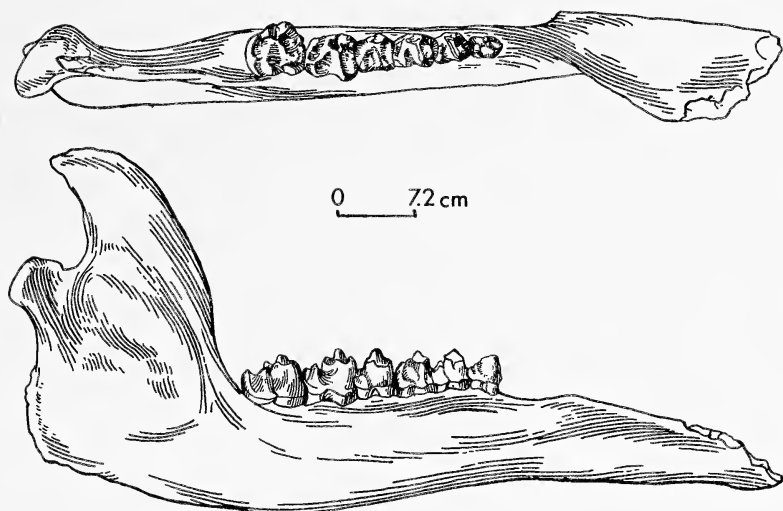


Fig. 19.—*Gobiatherium mirificum*. Paratype, AMNH 26630, lateral and crown views. The anterior alveolar border is restored from the left side (from Osborn and Granger, 1932).

poconulid forming posterior cingulum.  $M_1$ : similar to type specimen, but distance between hypoconid and hypoconulid longer, vertical crest of hypoconulid longer and posterior cingulum (formed by hypoconulid) wider.

**Discussion.**—The newly discovered specimens are similar to the type specimen, but because Osborn and Granger (1932) gave only a simple description of the type, a more complete description is given here.

The type specimen was found in the “Camp Margetts” area; that is, the present Huhe Bulak-Ulan Bulak area. V5709 was found in the Arshanto Obo area.

***Gobiatherium? major*, new species**  
(Fig. 23)

**Holotype.**—V5712, two broken lower jaws, associated, with left  $dP_3$  and  $M_1$  and right  $dP_4$ ,  $M_1$ , and  $M_3$  (posterior part) (field no. 1P<sub>3</sub>H<sub>8</sub>).

**Locality.**—Ulan Bulak.

**Diagnosis.**—Large size;  $M_1$  protoconid very prominent; “shelf” formed by  $M_3$  hypoconulid and entoconid very low, flat, not steep, and relatively wide.

**Description.**— $dP_3$ : larger than  $dP_4$ ; hypoconid crest relatively long; hypoconulid large and wide.  $dP_4$ : small; protoconid not prominent; almost no hypoconulid.  $M_1$ : large; protoconid very prominent; protolophid straight and wide; hypoconulid transversely wide.  $M_3$  (only posterior part): hypoconulid anteroposteriorly long, transversely wide and forming a wide “shelf”; entoconid distinct; hypoconulid crest and entoconid crest very weak.

**Discussion.**—This species differs from *G. mirificum* in that: 1)  $dP_4$  of *G. mirificum* is larger than  $dP_3$ , whereas  $dP_4$  of this species is smaller than  $dP_3$ ; 2) protoconid of *G. mirificum* is very weak or absent, whereas the protoconid of this species is large and prominent; 3) on  $M_3$  of *G. mirificum*, the hypoconulid and entoconid are very steep and form the posterior cingulum, whereas hypoconulid and entoconid in this species form a low, flat, wide shelf.

**Measurements.**—L/W:  $dP_3$ , 23.0/17.4? mm;  $dP_4$ , 19.5?/18.0 mm;  $M_1$ , 29.0/24.0 mm.

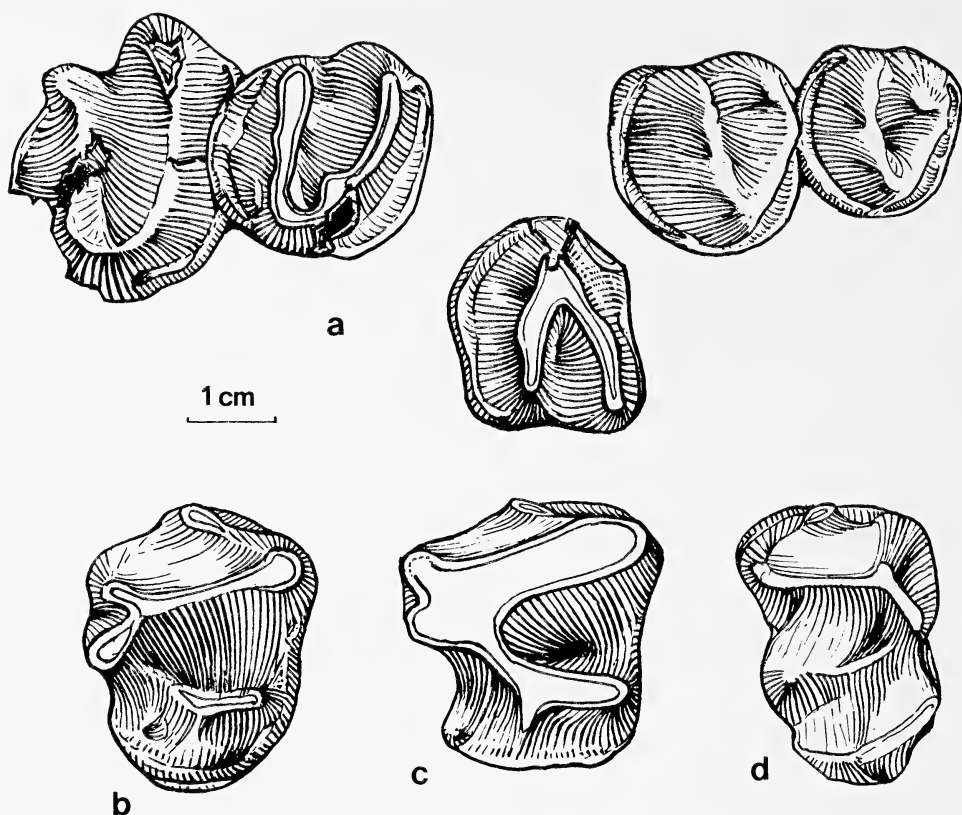


Fig. 20a-c.—*Gobiatherium mirificum*. (a) V5702, right  $P^{3-4}$ ,  $M^{2-3}$ , and left  $M^1$ ; (b) V5707, (c) V5706, both  $M_3$ . Fig. 20d. Cf. *Uintatherium* sp. V5711, right  $M_3$ .

***Gobiatherium? monolobotum*, new species**  
(Fig. 24)

*Holotype*.—V5713, 1-6:  $I_1$  ( $I_2?$ ), two  $I_3$  (partly broken); left  $P_2$  and  $P_3$ ,  $M_3$  (posterior part) (field no. 1P<sub>25</sub>H<sub>8</sub>).

*Referred specimens*.—V5713, 7-8: two incisors (field no. 77036-2).

*Localities*.—Ulan Bulak; Huhe Bulak.

*Diagnosis*.—Crown of incisor not notched.

*Description*.— $I_1$ : small; external wall smooth; straight crest from top to base on internal wall; top of crown pointed; no notch along crown edge.  $I_3$ : robust in size; in external view, crown caret-shaped; a relatively robust and straight crest runs from top to base on internal wall (another crest may parallel this crest, but this is not clear as tooth is broken).  $P_2$ : metaconid and metastylid distinguishable; relatively large.  $P_3$ : protoconid formed by protoconid, metaconid, and metastylid; direction of protoconid oblique to that of lower jaw; hypoconid prominent, extends forward forming oblique crest; oblique crest not joined to protoconid; posterior cingulum developed.  $M_3$ : protoconid robust; talonid long; hypoconulid very strong, but apex not pointed.

*Discussion*.— $P_2$  and  $P_3$  of this species are similar to those of *Gobiatherium mirificum*, but the incisors are quite different: the crown edge in *G. mirificum* is notched and the internal wall lacks a straight crest from the top to the base.  $M_3$  of *G. mirificum* also is larger than that of this species.



Fig. 21.—*Gobiatherium mirificum*. V5704, lower jaw with  $P_2$ – $M_2$ , crown and external views.

*Measurements*.—L/W:  $I_1$ , —/10.5? mm;  $I_3$ , 27.0/15.0 mm;  $P_2$ , 20.5?/14.0? mm;  $P_3$ , 22.0/16.5 mm;  $M_3$ , —/23.0 mm.

cf. *Uintatherium* sp.  
(Fig. 20d)

*Referred specimen*.—V5711, right  $M_3$  (field no. 1P<sub>5</sub>H<sub>8</sub>).

*Locality*.—Ulan Bulak.

*Discussion*.—In crown view  $M^3$  is apparently narrower than  $M^3$  of *Gobiatherium*, its paraconid is more prominent and its entoconid somewhat swollen.

*Measurements*.—L: 35.7 mm; W: 25 mm.

Order Perissodactyla Owen, 1848  
Suborder Tapiroidea Gill, 1872  
Family Isectolophidae Peterson, 1919  
*Homogalax* Hay, 1899  
***Homogalax reliquius*, new species**  
(Fig. 25)

*Holotype*.—V5748, right  $M_3$  (field no. 77036-2; L, 14.9 mm; W, 7.2 mm).

*Referred specimen*.—V5747, left  $M_3$  (field no. 77034; L, 15.3 mm; W, 6.8 mm).

*Locality*.—Huhe Bulak.

*Diagnosis*.— $M_3$  with single robust hypoconulid; metalophid well developed; trigonid relatively long.

*Description*.—V5748 ( $M_3$ ), crown wide anteriorly, narrow posteriorly, relatively high; posterior part of robust hypoconulid slightly turned toward lingual side; metalophid relatively well developed; tri-

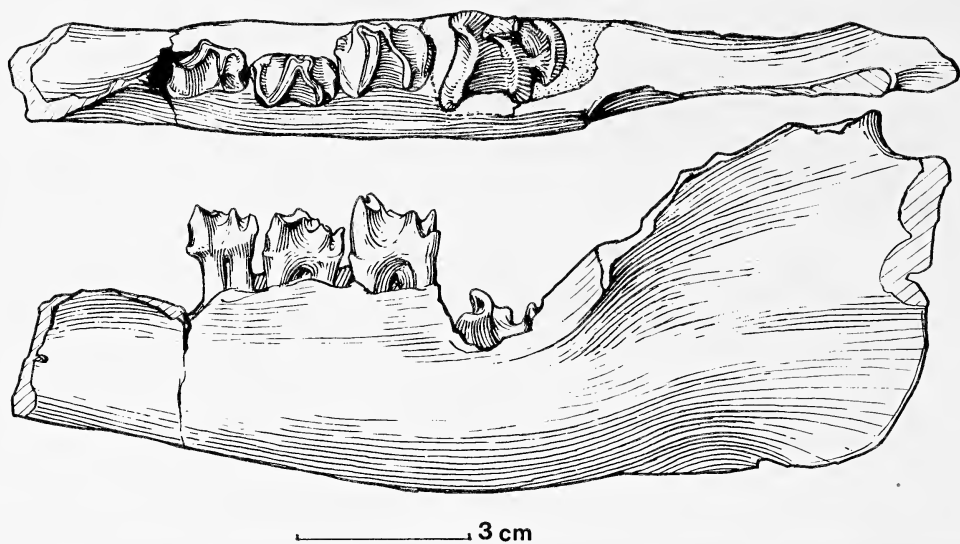


Fig. 22.—*Gobiatherium mirificum*. V5710, juvenile, lower jaw and cheek teeth, crown and external views.

gonid relatively long; weak development of cingulum at base of crown on labial side and behind hypoconulid.

The hypoconulid on V5747 ( $M_3$ ) consists of two cuspules, of which the labial one is larger than the lingual; crown relatively high; labial cingulum at base of crown weak.

*Discussion.*—These  $M_3$ s are unique among all Asiatic fossil tapirs because they have robust hypoconulids. The North American fossil tapirs *Homogalax* and *Isectolophus* bear robust hypoconulids. The former is early Eocene (Wasatchian), and the latter is middle and late Eocene (Bridgerian and Uintan). *Homogalax* is smaller than *Isectolophus*. On  $M_3$ , the hypoconulid of *H. protapirinus* is smaller than that of *I. latidens*, but the hypoconulid of *I. annectens* is still larger. The Inner Mongolian specimen is similar to *Homogalax*. The hypoconulid of V5747 ( $M_3$ ) consists of two cuspules, one labial, one lingual, whereas North American *Homogalax* may have an  $M_3$  with two cuspules, one anterior, and one posterior.

The metalophid of the Inner Mongolian specimen is separate from the protolophid, while that of *Homogalax* and *Isectolophus* is still connected with the protolophid. This indicates that the Inner Mongolian specimen was more bilophodont. Also, the Inner Mongolian specimen resembles North American *I. latidens* (such as AMNH 10640) in having a longer trigonid, but the former is higher crowned.

Family Helaletidae Osborn, 1892

*Heptodon* Cope, 1882c

*Heptodon minimus*, new species

(Fig. 26; Table 7)

*Holotype.*—V5732, associated lower jaws, with left  $P_1$ – $M_3$  and right  $P_2$ – $M_2$  (field no. 77036-2).

*Referred specimens.*—V5733: left lower jaw, with  $P_2$ – $M_3$  (77036-2); V5731, left  $M_3$  (77027).

*Locality.*—Huhe Bulak.

Table 6.—Measurements (mm) of *Gobiatherium mirificum*.

	V5702			AMNH 26624			V5707			V5710			AMNH 26622*		
	L	W		L	W		L	W		L	W		L	W	
P <sub>3</sub>	22.0	23.0		20.0	25.0										
P <sub>4</sub>	24.0	25.3		21.0	27.0										
M <sup>1</sup>	24.0	28.0		23.0	25.0										
M <sup>2</sup>	29.2	28.6		30.0	30.0										
M <sup>3</sup>	34.7	34.4		35.0	32.0										
M <sup>1-3</sup>	88.0 (ca.)			91.0											
	V5704			AMNH 26624			V5707			V5710			AMNH 26622*		
	L	W		L	W		L	W		L	W		L	W	
dP <sub>2</sub>	20.7	17.5		20.0	12.0					15.0	9.2				
P <sub>2</sub>															
dP <sub>3</sub>										15.8	10.0		17.0	10.0	
P <sub>3</sub>	24.2	16.3		23.0	18.0										
dP <sub>4</sub>										18.4	15.5		22.0	13.0	
P <sub>4</sub>	24.5	19.2		23.0	21.0										
M <sub>1</sub>	25.5?	21.6		28.0	23.0					26.0	20.5		24.0	22.0	
M <sub>2</sub>	31.8	29.4		31.0	29.0										
M <sub>3</sub>	39.2	34.0		39.0	34.0		37.5	35.2							
Depth, mandible below M <sub>1</sub>	66.0 (ca.)	67.0													

\* From Osborn and Granger (1932, Fig. 13).

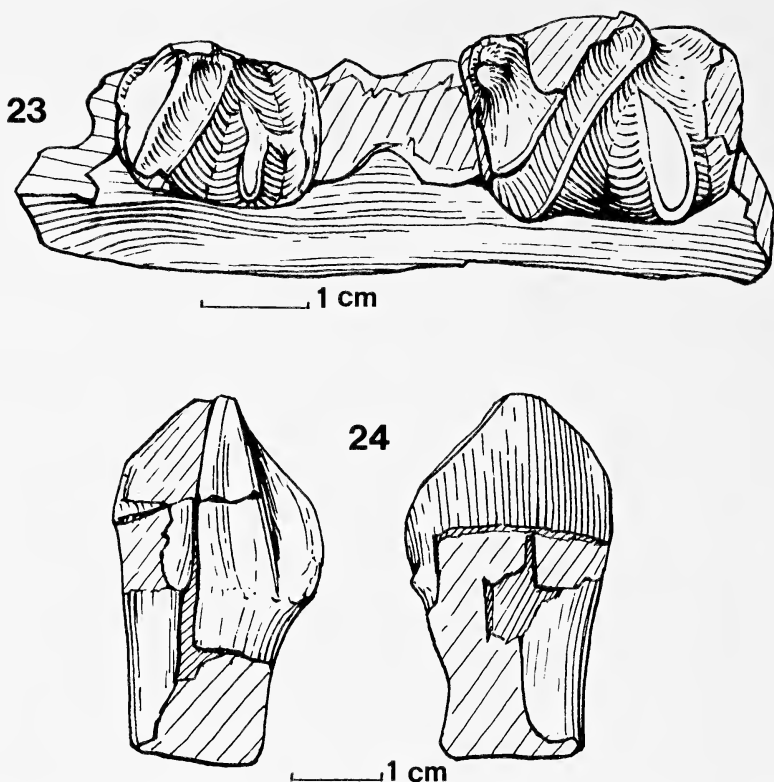


Fig. 23.—*Gobiatherium?* major new species. Holotype, V5712, right dP<sub>3</sub>, M<sub>1</sub>, crown view.

Fig. 24.—*Gobiatherium?* monolobotum new species. Holotype, V5713 (in part), incisor, internal and external views.

**Diagnosis.**—Main cusp on P<sub>2</sub> strong; P<sub>4</sub> entoconid present; hypoconulid of M<sub>3</sub> has two crests extending forward and connecting with hypolophid.

**Description.**—P<sub>1</sub> (V5732): protoconid high; posterior crest somewhat swollen; roots fused. V5733, P<sub>2</sub>: paralophid short; position of protoconid forward; metaconid not swollen; ectolophid relatively long, connecting with protolophid; entocristid distinct, also connecting with protolophid; no hypolophid; external cingulum extremely weak; no internal cingulum. P<sub>3</sub>: protoconid-paralophid-metaconid forming a semi-circle; ectolophid well developed and more lingual; entocristid connecting with metaconid; hypoconid small, not connecting with entoconid; external cingulum present; no internal cingulum. P<sub>4</sub>: metaconid not convex anteriorly, small notch between metaconid and protoconid; ectolophid developed; entocristid distinct; hypoconid small, not connecting with entocristid; external cingulum extremely weak; no internal cingulum. M<sub>1</sub>: paralophid distinct; metalophid short; hypoconulid triangular; external cingulum very weak; no internal cingulum. M<sub>2</sub>: triangular hypoconulid more prominent, connecting upward to top of hypolophid. M<sub>3</sub>: paralophid hooks ventrally; metaconid convex anteriorly; ectolophid relatively short; two crests extend from hypoconulid, a labial one anteroventrally, and a lingual one anterodorsally; a weak cristid crosses the hypoconulid valley antero-posteriorly.

**Discussion.**—The Inner Mongolian specimen (V5732) is quite different from North American earlier tapirs such as *Homogalax* and *Isectolophus*, being smaller, and bearing smaller hypoconulids.

Several North American tapirs such as *Helaletes*, *Dilophodon*, and *Colodon* have no P<sub>1</sub>, nor does the type specimen of *Heptodon calciculus* (AMNH 4858).

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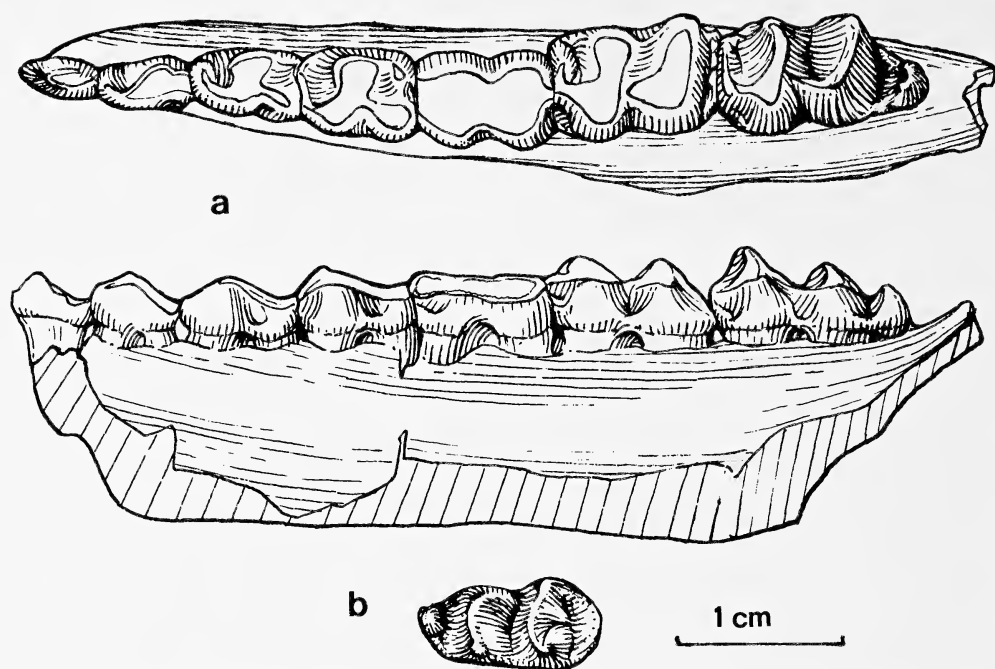


Fig. 26.—*Heptodon minimus* new species. (a) holotype, V5732 (in part), lower jaw with  $P_1$ – $M_3$ , crown and lateral views; (b) V5731,  $M_3$ .

*Locality*.—Ulan Bulak.

*Diagnosis*.—Metallophids of  $M_1$  and  $M_3$  relatively well developed,  $M_3$  short anteroposteriorly, its hypoconulid very small.

*Description*.— $P_4$ : paralophid relatively lingual and oriented anteroposteriorly; paraconid not swollen; metallophid relatively well developed; top of hypolophid located almost at level of talonid basin; no entoconid; no internal cingulum.  $M_1$ : hypoconid relatively well developed.  $M_2$ : paralophid very short; protolephid and hypolophid present; two segments of cingulum occurring on the external wall; no internal cingulum; hypoconulid flexed dorsally.  $M_3$ : paralophid relatively long; paraconid somewhat prominent; protolephid parallels hypolophid; metallophid extending forward and connecting with protolephid; hypoconulid small, but very distinct; buccal and lingual hypoconulid crests extend to base of hypolophid.

*Discussion*.—The position of the paralophid of  $P_4$  of this species, as in *H. mongoliensis*, is closer to the lingual margin of the crown than to the labial margin as in *Schlosseria magister* and *Lophialetes expeditus*. *H. medius* has a very small entoconid, so its talonid is nearly flat. On  $P_4$  in *Schlosseria magister* and *Lophialetes expeditus* the hypolophid is relatively well developed, but separated by a notch from the entoconid. An incomplete hypolophid occurs also in *Helaletes mongoliensis*, but the entoconid is stronger. In addition, *H. medius* is smaller. These features indicate that  $P_4$  of this species is more primitive in dental structure.

The hypoconulid of  $M_3$  of this species is very small, and the style of connection between the two crests extending from hypoconulid and hypolophid is similar to that in *Helaletes mongoliensis*. The hypoconulid of *H. mongoliensis* is larger, and the metallophids on the lower molars are not developed.

This species is similar to North American *Helaletes nanus* in size, but the trigonids of  $P_4$ – $M_3$  of the Inner Mongolian species are longer.



Table 8.—Measurements (mm) of *Helaletes medius*, *H. mongoliensis*, and *H. nanus*.

	<i>Helaletes medius</i>				<i>Helaletes mongoliensis</i> AMNH 20155		<i>Helaletes nanus</i> (Radinsky, 1963)	
	V592		V5730		L	W	L	W
	L	W	L	W				
P <sub>3</sub>	6.5?				9.75	7.30	6.8–8.7	4.5–5.9
P <sub>4</sub>	8.9	6.3			10.00	8.77	7.5–8.8	5.1–7.0
M <sub>1</sub>	9.1?	6.8			12.28	9.05	8.4–10.8	5.3–7.3
M <sub>2</sub>	11.8	8.0	11.4	8.5	14.55	10.35	9.9–11.8	6.3–7.9
M <sub>3</sub>	14.5	8.2	15.0	8.1	17.50	10.30	11.5–11.1	6.5–8.3
M <sub>1–3</sub>	36.4	35.4?						

*Helaletes fissus* (Matthew and Granger, 1925)  
(Fig. 28)

*Holotype*.—AMNH 20161, maxillary fragment with P<sup>2–4</sup>.  
*Locality*.—Near Camp Margetts.  
*Diagnosis*.—“Slightly smaller than *Helaletes mongoliensis*, with P<sup>2–4</sup> relatively shorter and wider, and hypocones better separated from protocones than in that species. P<sup>2–4</sup> metalophs not so prominent as protolophs, and directed toward protocones” (Radinsky, 1965, p. 230).  
*Discussion*.—Radinsky (1965) referred *Desmatotherium fissum* to *Helaletes fissus*, a new combination, and, although the geological position of this species was not clear at that time, Radinsky suggested that *H. fissus* and *H. mongoliensis* may occur in different horizons. His suggestion has proven to be correct.  
It is not possible to make comparisons between *H. fissus* and *H. medius* because the former has only P<sup>2–4</sup> and latter only lower cheek teeth. However, as Radinsky (1965, p. 231) pointed out, “The upper premolars of *Helaletes fissus* are more advanced than those of any other species of *Helaletes* . . .” The relatively primitive lower premolars of *H. fissus* suggest that it and *H. medius* are not the same species.

*Helaletes fissus?* (Radinsky, 1965)

*Discussion*.—The features of AMNH 81802 (C<sub>1</sub>–M<sub>3</sub>) studied by Radinsky (1965, p. 231) are advanced for *Helaletes* although “It is slightly smaller than *Helaletes mongoliensis* and agrees in size with the type of *H. fissus*.” The P<sub>3–4</sub> of *Helaletes fissus?* have small entoconids, but nothing on P<sub>4</sub> is suggestive of *Helaletes medius*.

*Hyrachyus* Leidy, 1871  
*Hyrachyus neimongoliensis*, new species  
(Fig. 29)

*Holotype*.—V5721: an incomplete skull, with left P<sup>2</sup>, P<sup>4</sup>, M<sup>1</sup> (partly broken), and M<sup>2–3</sup> (field no. 77036-2).  
*Locality*.—Huhe Bulak.  
*Diagnosis*.—Frontal bone and nasal bone flat and straight; hypsodont; parastyles on molars very strong; paraloph almost parallel to metaloph; premolars non-molariform.  
*Description*.—Skull: height low; posterior part of premaxilla narrow, body ascending abruptly, not gently; nasal bone flat and straight; posterior edge of nasal notch just anterior to P<sup>2</sup>; position of orbit low; frontal bone wide and flat; maxilla very long; zygomatic process of temporal bone and zygomatic process of molar bone join in mid part of zygomatic arch; zygomatic arch very long; suture between

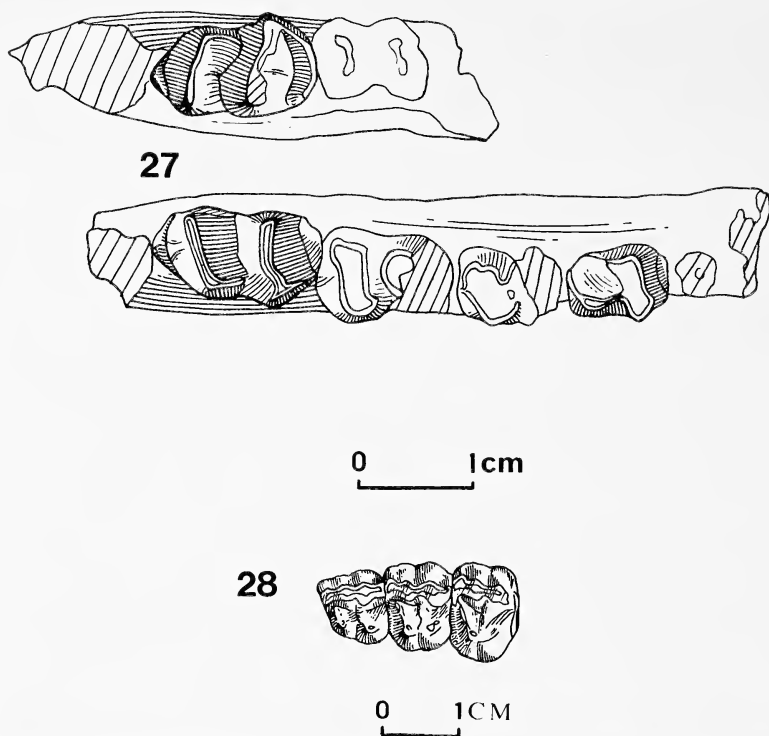


Fig. 27.—*Helaletes medius* new species. Holotype, V5729, lower jaws with left  $M_3$  and right  $P_4$  and  $M_3$ .

Fig. 28.—*Helaletes fissus*. AMNH 20161,  $P^{2-4}$  (from Matthew and Granger, 1925c).

parietal and interparietal present; palatine process of maxilla narrow; median palatine suture clear; horizontal part of palatine narrow; basilar tubercles evident, separating basilar part of occipital and body of sphenoid; alar canal distinct; paramastoid process relatively large; mastoid process and occipital condyle relatively small; foramen magnum relatively large.

Upper cheek teeth:  $P^3$ : paraloph connecting with ectoloph and protocone; attachment of paraloph and ectoloph lower than apex of protocone; hypocone distinct; metaloph connecting with ectoloph, and attachment of the two lophs higher than that of protoloph and ectoloph; anterior cingulum stronger than posterior cingulum; no external cingulum; paracone high, forming a rib-like and relatively robust crest on external wall; ectoloph straight.  $P^4$ : larger than  $P^3$ ; protocone robust, forming paraloph, which connects to ectoloph; paracone more prominent than metacone; two rib-like crests formed by these cusps on external wall (that is, anterior rib and posterior rib); anterior rib stronger than posterior rib; metaloph short, not connecting with paraloph; ectoloph straight; anterior cingulum distinct; no external cingulum.  $M^1$ : (anterior part broken) middle part of paraloph swollen, may be result of wear of massive antecrochet; metacone long; angle between metacone and metaloph about  $90^\circ$ ; external wall of metacone flat and straight; anterior cingulum more distinct than posterior one.  $M^2$ : largest of cheek teeth; paraloph robust; metaloph short; posterior part of ectoloph straight; paracone high; parastyle relatively robust; anterior cingulum clearer than posterior cingulum; no external cingulum; the angle between metacone and metaloph about  $60^\circ$ .  $M^3$ : distance between paraloph and metaloph large, these two lophs almost parallel; paracone prominent; parastyle relatively strong; metacone (crest) short; angle between metacone and metaloph about  $90^\circ$ ; anterior cingulum wider than posterior cingulum.

*Discussion.*—Wood (1934, p. 189) pointed out the diagnostic features of *Hyrachyus*: “Hornless; protoloph of upper molars much more prominent than the metaloph; no tendency for the metalophs of the upper premolars to touch the crista; attachments of upper premolar metalophs to ectolophs usually higher than

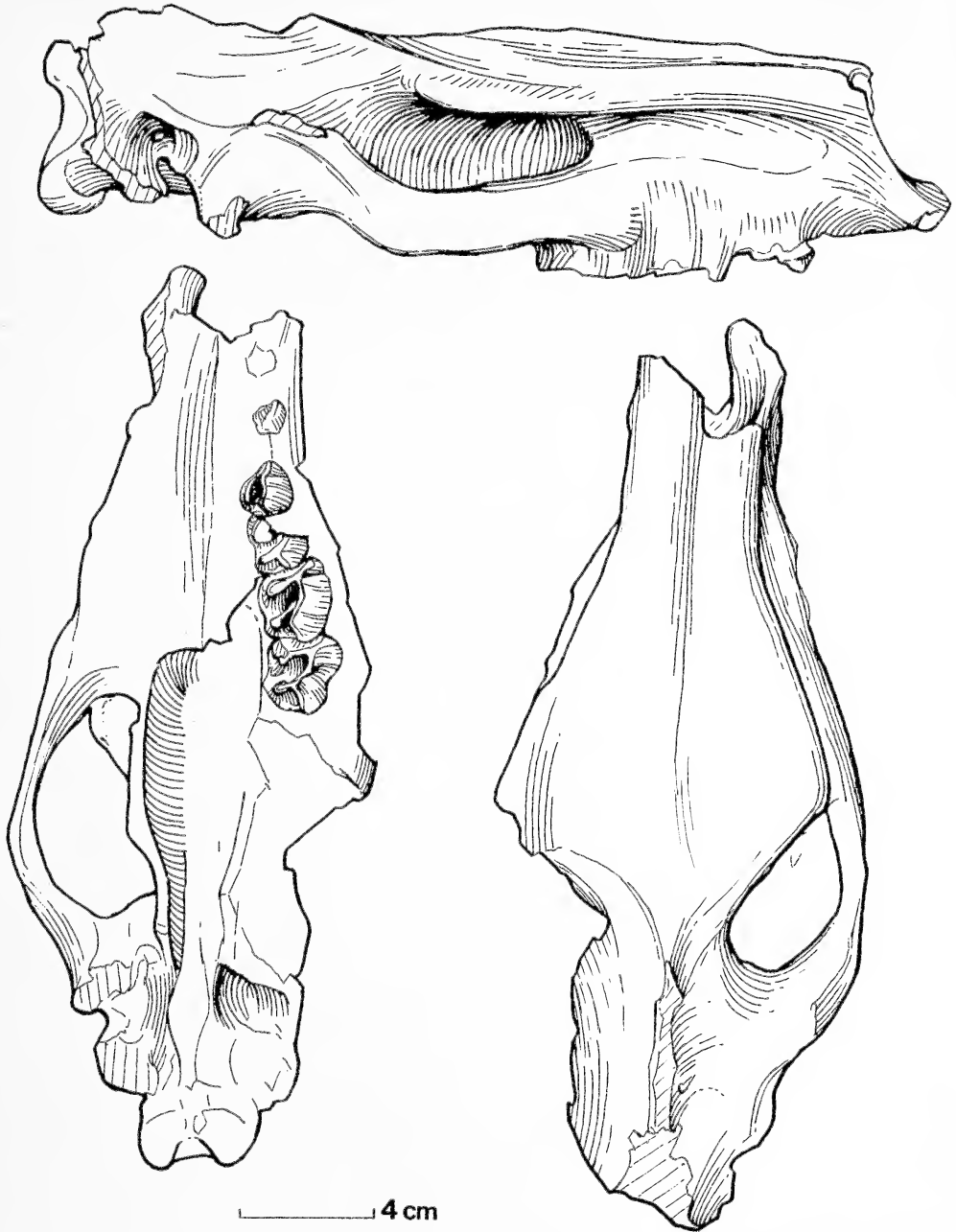


Fig. 29.—*Hyrachyus neimongoliensis* new species. Holotype, V5721, skull, lateral, palatal, and dorsal views.

corresponding attachments of the protolophs; upper cheek teeth subrhinocerine rather than rhinocerine, except after extreme wear.”

Radinsky (1967a, p. 21) also pointed out that *Hyrachyus* is: “A conservative group preserving into the Middle Eocene primitive dental and skeletal features

Table 9.—*Measurements (mm) of Hyrachyus crista.*

	V5722		V5723	
	L	W	L	W
P <sup>4</sup>	13.5	17.5	14.5	18.3
M <sup>1</sup>	17.5	19.0	19.2	20.0
M <sup>2</sup>	21.4	21.4	23.5	22.6
M <sup>3</sup>	18.4	19.0		
M <sup>1-3</sup>	55.0			

seen in the earliest *Heptodon*. Incisors spatulate. Postcanine diastema present. P<sub>1</sub> retained; premolars non-molariform to submolariform. No tendency toward bilophodonty. M<sub>3</sub> without a hypoconulid. No nasal incision enlargement."

Unquestionably, the Inner Mongolian species is very close to the North American *Hyrachyus eximius* (= *H. princeps*, AMNH 12364). Both species have some similar characters in both skull and cheek teeth: 1) P<sup>4</sup>: attachments of metaloph to ectoloph higher than corresponding attachment of protoloph; 2) M<sup>3</sup>: parastyles strong, and paraloph is close to and almost parallels metaloph. The species have some differences: 1) the P<sup>4</sup> of the Inner Mongolian species has no crochet, while the North American P<sup>4</sup> does; 2) widths of the molars of the North American specimen are greater than lengths, while the Inner Mongolian specimen has the opposite condition.

M<sup>3</sup> of *Hyrachyus metalophus* (Zhou and Qi, 1982) is somewhat smaller than this species, but has a very prominent external rib on the ectoloph. This is a primitive character.

The skull of this species bears some resemblance to that of *Forstercooperia huhebulakensis*: skull dimension; skull low and flat; zygomata slender; and the position of the bulla.

*Measurements.*—Skull: length between premaxilla and condyles, 365 mm; width, across zygomatic arch, 158 mm; depth of skull above M<sup>3</sup>, 81 mm; width of skull (postorbital constriction), 52 mm; width of condyles, 51 mm. Upper cheek teeth (L/W): P<sup>2</sup>, 12.3/12.3 mm; P<sup>4</sup>, 16.1/21.3 mm; M<sup>1</sup>, 26 (ca.)/21 mm (ca.); M<sup>2</sup>, 30.5/27.3 mm; M<sup>3</sup>, 28.4/26.2 mm; (L): M<sup>1-3</sup>, 77.0 mm (ca.).

### *Hyrachyus crista*, new species

(Fig. 30; Table 9)

*Holotype.*—V5722, fragmentary maxilla with P<sup>4</sup>–M<sup>3</sup> (field no. 77031).

*Referred specimen.*—V5723, fragmentary maxilla with left and right P<sup>4</sup>–M<sup>2</sup> (right P<sup>3</sup> broken) (77031).

*Locality.*—Bayan Ulan.

*Diagnosis.*—Attachment of P<sup>4</sup> metaloph to ectoloph higher than corresponding attachment of protoloph; internal cingulum distinct at the base of protocone; crochet on P<sup>4</sup>–M<sup>2</sup> very weak, but distinct on M<sup>3</sup>.

*Description.*—P<sup>3</sup> (V5722, same below); only three alveoli remaining. P<sup>4</sup>: attachment of metaloph to ectoloph higher than corresponding attachment of protoloph; paracone and metacone forming two clearly rib-like crests (anterior rib and posterior rib); parastyle prominent; internal cingulum distinct at the base of protocone; crochet weak. On P<sup>4</sup> of V5723, no crochet, internal cingulum forming indistinct semi-circle. M<sup>1</sup>: parastyle prominent; paracone high, forming anterior rib; metacone relatively long, posterior rib very weak; ectoloph connected to metaloph, but attachment covered by cement; angle between metacone (crest) and metaloph smaller than 90°; metaloph higher than paraloph; external cingulum weak and short at the base of metacone; crochet very weak. On M<sup>1</sup> of V5723, posterior rib very weak; internal side of parastyle notched; no crochet. M<sup>2</sup>: similar to M<sup>1</sup>, but parastyle stronger, crochet clearer, metacone longer. On M<sup>2</sup> parastyle on V5723 notched. M<sup>3</sup>: parastyle notched, not as

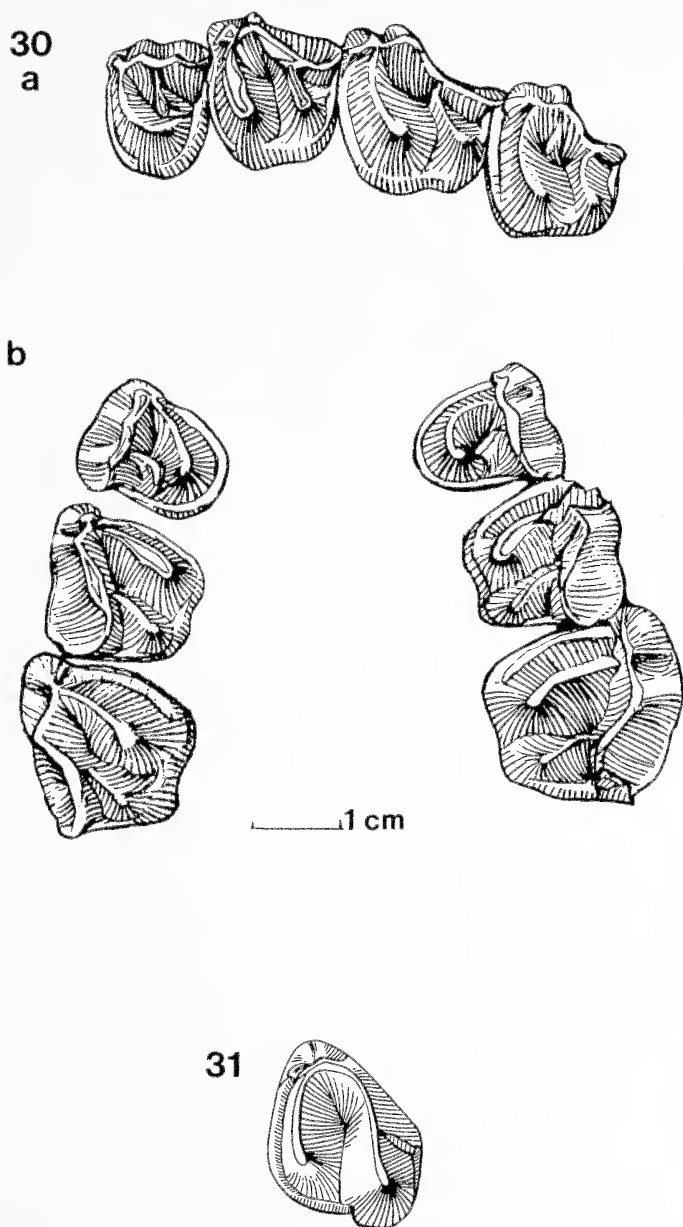


Fig. 30.—*Hyrachyus crista* new species. (a) Holotype, V5722, P<sup>4</sup>-M<sup>3</sup>; (b) V5723, left and right P<sup>4</sup>-M<sup>2</sup>.

Fig. 31.—*Hyrachyus* sp. cf. *H. eximius*. V5728, left M<sup>3</sup>.

robust as on M<sup>2</sup>; crochet distinct; metacone straight; paraloph not close to metaloph but parallel to it; paracone high, forming prominent anterior rib.

*Discussion.*—Radinsky (1967a) referred one genus, *Hyrachyus*, to the Subfamily Hyrachyinae, and three species: *H. modestus* from North America, Europe, and China; *H. eximius* from North America and possibly from China; and *H. minimus* from North America.

Radinsky's (1967a, p. 22) diagnoses of these species are as follows:

1) *H. modestus*: "A small to medium-sized *Hyrachyus* species: mean length of  $M^{1-3}$  from about 45 to 50 mm. Premolars non-molariform. Upper molars usually lack lingual and labial cingula."

2) *H. eximius*: "Size large: mean length of  $M^{1-3}$ , 64 mm. Premolars non-molariform. Upper molars usually lack lingual and labial cingula."

3) *H. minimus*: "A medium-sized *Hyrachyus* species: mean length of  $M^{1-3}$ , about 50 mm. Premolars submolariform. Upper molars usually with labial and lingual cingula.  $M^3$  metacone situated more labially than in other *Hyrachyus* species. In these features *H. minimus* is intermediate between other *Hyrachyus* species and *Chasmothereium cartieri*."

$P^4$  of the Inner Mongolian species is similar to *Hyrachyus modestus*, especially between V5722 and AMNH 12667. Both  $P^4$ s have very prominent anterior and posterior ribs, and very prominent anterior and posterior cingula. Some different characters are apparent also on various  $P^4$ s of *H. modestus*: 1) V5722 and AMNH 80183 have crochets, while V5723 and AMNH 12667 have no crochets; 2) V5723 has a semi-circle-like internal cingulum, lacking on AMNH 12667.  $M^{1-3}$  of the Inner Mongolian species are different from those of *Hyrachyus modestus* in the following points: 1) parastyle relatively small; 2) higher crown; 3) metacone elongated.

Apparently the genus *Hyrachyus* not only appeared in Asia, but its later members were broadly distributed in east Asia. *Hyrachyus modestus* appears closely related to *H. crista*.

*Hyrachyus* sp. cf. *H. eximius*  
(Fig. 31)

*Referred specimen*.—V5728: left  $M^3$  (field no. 77039).

*Locality*.—Huhe Bulak.

*Discussion*.—This tooth is similar to  $M^3$  of *Hyrachyus eximius* (AMNH 12362) found in Bridger C beds, Wyoming. The main similarities are: 1) paraloph parallel to metaloph; 2) paraloph not close to metaloph; 3) degree of hypsodonty; 4) length/width ratio. The metacone of the Inner Mongolian specimen is weaker.

Compared to  $M^3$  of *Colodon inceptus* (found in Inner Mongolia), the  $M^3$  referred here is wider, and the attachment of the paraloph to the ectoloph is closer to that of the metaloph to the ectoloph. Both  $M^3$ s have short metacones.

*Measurements*.—(V5728):  $M^3$  (L/W), 14.4/22.0 mm.

*Hyrachyus* sp.  
(Fig. 32)

*Referred specimens*.—V5724, left  $M^{2-3}$  (field no. 77028H<sub>2</sub>); V5725, right  $P^4$  (77036-2); V5726, right  $P^4$  (77036-2); V5775, left  $M^3$  (77039); V5776, right  $M^3$  (77039).

*Localities*.—Daatein Obo, Huhe Bulak.

*Discussion*.—These specimens, collected from several sites, are too incomplete to be assigned with certainty. V5724 was found in Daatein Obo Cliff along with other fossil mammals, *Microtitan? elongatus*, *Forstercooperia grandis* and *Asiomys medius*. Characters of the two molars are as follows:  $M^2$ : parastyle, a slender, prominent pillar; paracone high, forming a clear anterior rib; metacone long,

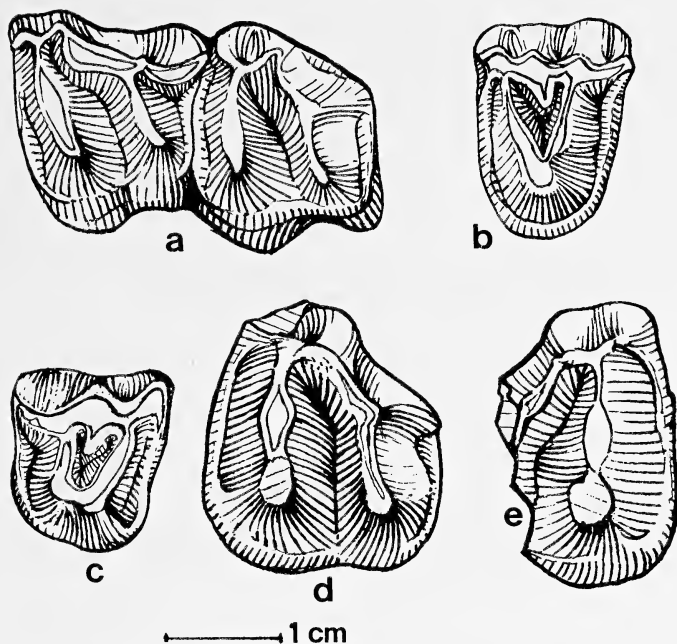


Fig. 32.—*Hyrachyus* sp. (a) V5724, M<sup>2-3</sup>; (b) V5725, P<sup>4</sup>; (c) V5726, P<sup>4</sup>; (d) V5775, M<sup>3</sup>; (e) V5776, M<sup>3</sup>.

without a clear posterior rib; cingulum around the base of the crown (except anterior edge); no crochet. M<sup>3</sup>: parastyle as on M<sup>2</sup> and separate from protocone; attachment of paraloph to ectoloph close to that of metaloph; metacone relatively long; anterior cingulum clear. M<sup>2-3</sup> are similar to those of *H. crista* but they are smaller, have weaker parastyles that are slender, pillar-like and separate from the protocone, and lack a crochet on M<sup>3</sup>. Among these characters, the slender pillar-like parastyles are rarely seen in tapiroids.

On P<sup>4</sup> (V5725 from the Irдин Manha beds) the paracone is very close to the metacone; the crochet is very well developed; the paraloph is not connected to the ectoloph and is relatively straight (the paraloph of *H. crista* is somewhat curved and hook-shaped); its metaloph is swollen as in *H. crista*.

P<sup>4</sup> (V5726 from the Arshanto beds), in crown view, is nearly square, the crochet is strong, the metacone relatively long, and the paraloph is longer than and connected to the metaloph. This tooth differs from P<sup>4</sup> of *Schlosseria magister* in its larger size; nearly square occlusal outline, strong crochet, and long metacone (crest). The length/width ratio of V5726 (P<sup>4</sup>) differs from that of North American *Hyrachyus modestus*. Also, the P<sup>4</sup> metaloph of *H. modestus* is isolated, that is, not connected to the paraloph. The attachment of paraloph to ectoloph in V5726 is higher than the corresponding attachment of metaloph, in contrast to the usual condition.

V5775 (M<sup>3</sup>) and V5776 (M<sup>3</sup>) were found in Huhe Bulak area, and are *Hyrachyus*-like in that the paraloph of V5775 parallels the metaloph.

*Measurements.*—L/W (mm): M<sup>2</sup> (V5724), 17.0/18.3; M<sup>3</sup> (V5725), 14.5/17.4; P<sup>4</sup> (V5726), 13.2/18.7; M<sup>3</sup> (V5775), 20.0/22.1; M<sup>3</sup> (V5776), 23.0.

Table 10.—Measurements (mm) of Schlosseria magister.

	AMNH 20241		V5734		V5735		V5736		V5740		V5738	
	L	W	L	W	L	W	L	W	L	W	L	W
P <sup>1</sup>	5.8	4.6										
P <sup>2</sup>	6.45	7.8										
P <sup>3</sup>	8.17	9.9			7.4	9.7					11.3?	11.3
dP <sup>4</sup>												
P <sup>4</sup>	8.4	10.6	8.5	10.7	8.0	10.5			7.9	10.5		
M <sup>1</sup>	10.6	12.0	10.6	11.6	10.3	12.0			9.3	11.9		
M <sup>2</sup>	11.7	13.15	11.4	12.4	12.8?	12.2?	12.3	14.2	11.9	12.0		
M <sup>3</sup>			10.5	11.5			11.7	13.0	10.9	11.4		
M <sup>1-3</sup>	10.83	12.36	32.2						32.0			
	AMNH 20242-20245		V5734		V5743		V5741		V5737		V5745	
	L	W	L	W	L	W	L	W	L	W	L	W
C <sub>1</sub>					5.4	3.5						
I <sub>3</sub>					5.9	3.0						
P <sub>1</sub>	5.1		2.4								5.3	
P <sub>2</sub>	6.2		3.4		6.6	4.0						8.4 4.0
dP <sub>3</sub>												
P <sub>3</sub>	8.6	6.15	7.8	5.3	8.2	5.5	7.7	5.9				9.4 4.6
dP <sub>4</sub>												
P <sub>4</sub>	8.9	6.55	7.8	6.0	8.2	6.2	8.1	6.5				
M <sub>1</sub>	10.6	7.6	10.0	7.0	10.2	7.0	9.3	8.0	10.0	7.2		
M <sub>2</sub>	11.5	7.95	11.0	7.4	11.1	7.7	10.4	8.0	10.9	8.9		
M <sub>3</sub>	15.2	7.5	15.4	7.0	14.8	7.2	15.0	7.6	15.2	7.5		
P <sub>1-4</sub>			2.6 (ca.)		27.3 (ca.)							
P <sub>1</sub> -M <sub>3</sub>			62.5 (ca.)		62.5 (ca.)							
M <sub>1-3</sub>	36.5		35.8		35.8		34.9		35.2			
Diastema	14.8		14.0 (ca.)		14.0 (ca.)							
Depth of mandible below M <sub>1</sub>	17.8				19.0 (ca.)		17.2					



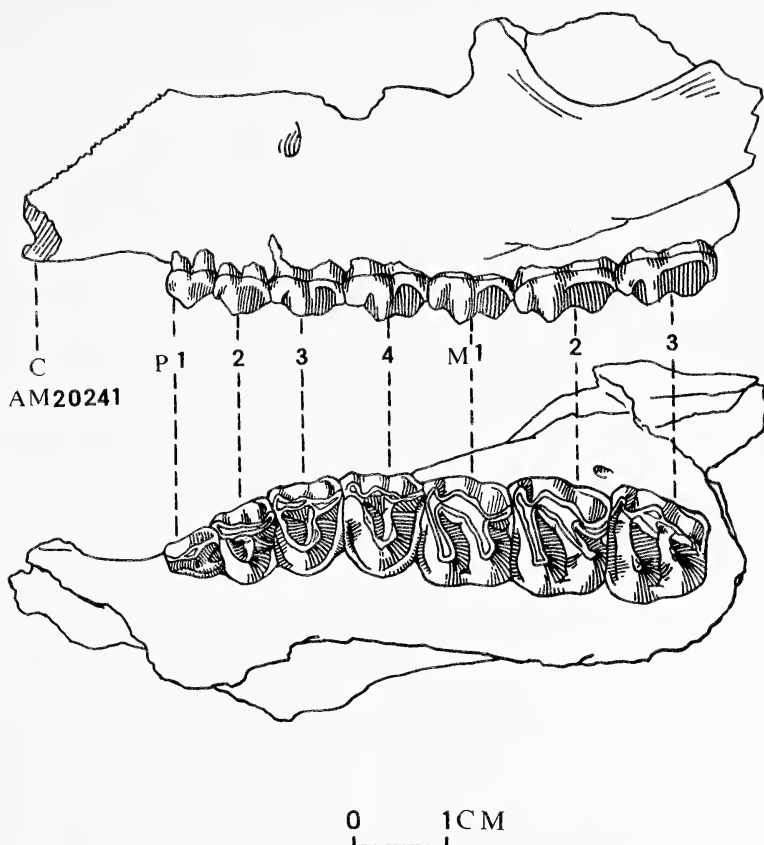


Fig. 33.—*Schlosseria magister*. Holotype, AMNH 20241, P<sup>1</sup>–M<sup>1</sup> (from Matthew and Granger, 1926).

Family Lophialetidae Radinsky, 1965  
*Schlosseria* Matthew and Granger, 1926  
*Schlosseria magister* Matthew and Granger, 1926  
 (Figs. 33, 34; Table 10)

*Holotype*.—AMNH 20241, upper and lower jaws, fore and hind feet.

*Referred specimens*.—V5734, associated maxillae with left and right P<sup>4</sup>–M<sup>3</sup>, lower jaw with P<sub>2</sub>–M<sub>3</sub> (with P<sub>1</sub> alveoli); V5735, maxilla with P<sup>3</sup>–M<sup>2</sup>; V5736, maxilla with M<sup>2-3</sup>; V5737, lower jaw with M<sub>1-3</sub>; V5738, maxilla with dP<sup>4</sup>–M<sup>2</sup> (field no. 77039); V5739, right M<sup>3</sup>; V5740, maxilla with P<sup>2</sup>–M<sup>3</sup>; V5741, lower jaw with P<sub>3</sub>–M<sub>3</sub> (77036-2); V5742, 1–10, cheek teeth; V5743, lower jaw with left I<sub>3</sub>, P<sub>2</sub>–M<sub>3</sub> and right C, P<sub>2</sub>–M<sub>1</sub>; V5744, dP<sub>3-4</sub>; V5745, lower jaw with P<sub>1</sub>, P<sub>3</sub>, and P<sub>4</sub> (77034).

*Localities*.—Irdin Manha area and Huhe Bulak.

*Discussion*.—Of the known fossil mammals in the Arshanto beds, *Schlosseria magister* is most abundant. It occurs throughout the Arshanto beds in the Huhe Bulak and Ulan Bulak areas. After studying Morris' field notes for 1923 and 1925, Radinsky (1964, p. 3) determined the precise location of the type locality: "the *Schlosseria* quarry . . . for the distance from it to Arshanto well is recorded as 3 miles . . . ."

Radinsky (1965, p. 197) found that, "In the Irdiv Manha area the beds containing *Schlosseria* underlie those with *Lophialetes*, but in the Camp Margetts area both genera are recorded as coming from the same horizon." Our discoveries have confirmed this point at least in the Huhe Bulak (that is, Camp Margetts) area. In Radinsky's study of the early Tertiary Tapiroidea of Asia, he listed the differences between *Schlosseria* and *Lophialetes*, as follows: species of *Schlosseria* are "Medium sized lophialetids with premolar series long relative to molar series. Premolar and molar metacones short and slightly convex; lophs and lophids relatively low and obtuse. P<sup>1</sup> with narrow posterolingual shelf. P<sup>2-4</sup> with protoloph-metaloph loop. M<sup>2-3</sup> relatively short and wide. P<sub>2-3</sub> relatively long and narrow, with long trigonids. Nasal incision not so enlarged as that in *Lophialetes*. Manus tridactyl" (Radinsky, 1965, pp. 199-200).

Although the new specimens are very similar to *Schlosseria magister* and differ from *Lophialetes expeditus*, the two genera share some characters and occur in the same beds. Therefore, the possibility should not be excluded that these are sexual differences. This needs more detailed study.

Ranga Rao (1972) described a new tapiroid, *Kalakotia*, and made detailed comparisons between *Kalakotia* and *Schlosseria* (or *Lophialetes*). Although there exist several apparent differences between these genera, such as *Kalakotia* being smaller in size and more primitive in tooth pattern, Rao referred this genus to the Lophialetidae because, "it is clear that *Kalakotia* bears more similarities in dental structure to the Mongolian forms: *Lophialetes* and *Schlosseria*, than to any other known tapiroid."

*Schlosseria* sp. cf. *S. magister*  
(Fig. 35)

*Referred specimen.*—V5746, right M<sub>3</sub> (field no. 77034).

*Locality.*—Huhe Bulak.

*Discussion.*—On this M<sub>3</sub>, two small crests extend from the hypoconulid and attach to hypolophid in a manner similar to that in *S. magister*. At the base of hypoconulid, labially, there is a cingulum that is not present in other species of *Schlosseria*, but the tooth is similar otherwise to Radinsky's (1965) *Schlosseria* cf. *Schlosseria magister*.

*Measurements.*—(V5746) L/W: 13.6/6.7 mm.

*Lophialetes*  
*Lophialetes expeditus* Matthew and Granger, 1925  
(Figs. 36, 37; Table 11)

*Holotype.*—AMNH 19163, maxilla with P<sup>1</sup>–M<sup>3</sup>.

*Referred specimens.*—V5749, left M<sup>1</sup>; V5750, right M<sup>3</sup>; V5751, maxilla with dP<sup>2-3</sup> (field no. 77027); V5752, left M<sup>2</sup>; V5753, maxilla with dP<sup>3</sup>–M<sup>1</sup> (field no. 77036-2); V5754, maxilla with left dP<sup>1</sup> (broken)–M<sup>1</sup> and right dP<sup>3-4</sup> (broken); V5755, jaw with left dP<sub>2</sub>–M<sub>1</sub> and dP<sub>3</sub>–M<sub>1</sub>; V5756, lower jaw with dP<sub>3</sub> and M<sub>3</sub> (field no. 77039).

*Localities.*—Camp Margetts; Huhe Bulak.

*Description.*—dP<sup>1</sup> (V5754, largely broken): only the ridged internal edge can be seen. dP<sup>2</sup> (V5754): paraloph oblique, not parallel to metaloph; hypocone strong; metaloph straight; paracone high; crochet relatively clear; cingulum extremely weak. dP<sup>3</sup>: paraloph straight and long; the position of metaloph higher than paraloph; paracone and metacone very prominent; paracone rib and metacone rib clear; parastyle prominent; crochet relatively distinct; metastyle slightly prominent. dP<sup>4</sup>: paraloph long; a small crest between parastyle and paracone; paracone rib stronger than metacone rib; on left dP<sup>4</sup> a

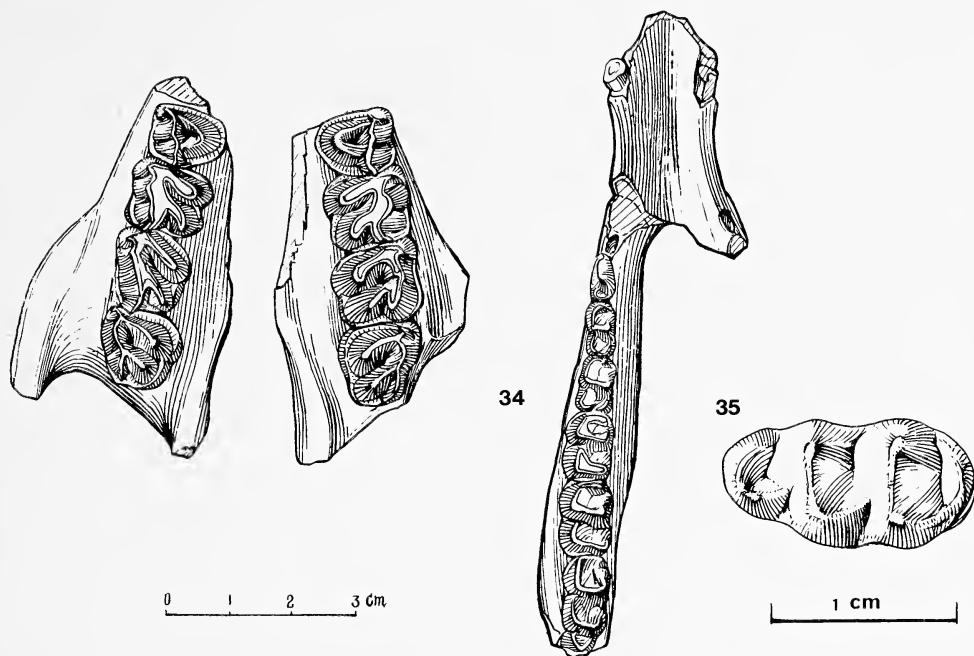


Fig. 34.—*Schlosseria magister*. V5734, palate with right and left  $P^4$ – $M^3$  and lower jaw with C,  $P_2$ – $M_3$ .

Fig. 35.—*Schlosseria* sp. cf. *S. magister*. V5746, right  $M_3$ .

secondary cuspule occurs at the base of hypocone.  $dP_1$  (V5755), single-rooted.  $dP_2$ : paraconid small but distinct; protolophid straight; protoconid highest cusp; metaconid close to paraconid; metalophid distinct.  $dP_3$ : paraconid very prominent; paraconid not close to metaconid; protolophid relatively long; entoconid prominent, connects with hypoconid forming hypolophid; a small triangle-like process at position of hypoconulid.  $dP_4$ : in crown view wider anteriorly than posteriorly; metaconid strong and convex anteriorly; distance from protoconid to anterior edge of tooth shorter than on  $dP_3$ ; triangle-like process at hypoconulid position more prominent.

**Discussion.**—The differences between *Schlosseria* and *Lophialetes* were mentioned above. These new specimens are unquestionably *Lophialetes*. The milk teeth reported by Radinsky (1965) are also quite similar to the new specimens.

*Breviodon* Radinsky, 1965

*Breviodon minutus* (Matthew and Granger, 1925)

(Figs. 38, 39, 40; Table 12)

*Breviodon acares* Radinsky, 1965, p. 203.

**Holotype.**—AMNH 20139, upper molar.

**Referred specimens.**—AMNH 26113 (holotype of *Breviodon acares*), left mandible with  $I_3$  (reversed),  $C_1$ ,  $P_3$  alveolus, and  $P_4$ – $M_3$ ; V5757, maxilla with  $dP^{3-4}$  and  $M^1$ ; V5758,  $dP^{3-4}$  (above field no. 77027); V5759, low jaw with  $M_{1-2}$  (broken) ( $1P_{25}H_8$ ); V5760, low jaw with  $dP_4$  (broken) and  $M_1$  ( $1P_{25}H_8$ ).

**Localities.**—Irdin Manha area (type locality of *B. minutus*), Ulan Bulak, Huhe Bulak, North Mesa, Ulan Shireh (type locality of *B. acares*).

**Description.**— $dP^3$ : in crown view nearly square; paraloph almost parallel to metaloph; paracone rib and metacone rib distinct; posterior cingulum very weak; no cingulum at the base of hypocone.  $dP^4$ : similar to  $dP^3$ , but paraloph more prominent; metacone flat and straight.  $M^1$ : larger in size; lophs

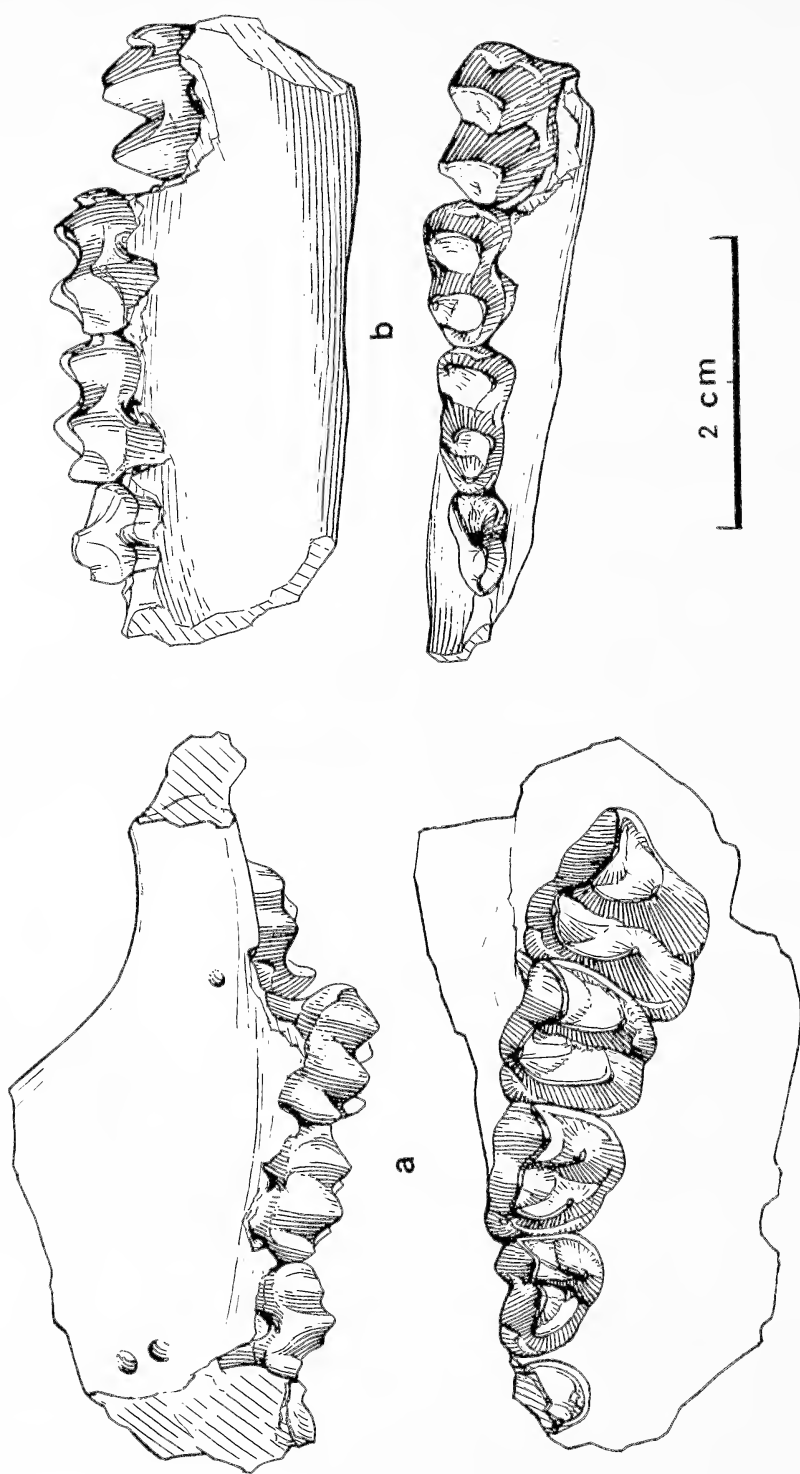


Fig. 36.—*Lophialetes expeditus*. (a) V5754, maxilla with dP<sup>1</sup>–M<sup>1</sup>; (b) V5755, jaw with left dP<sup>2</sup>–M<sup>1</sup>.

Table 11.—Measurements (mm) of *Lophialetes expeditus*.

	V5754		V5754 (left)		V5755		V5753		V5749		V5752		V5750	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
dP <sup>1</sup>	6.0?	4.7												
dP <sup>2</sup>	7.8	7.3												
dP <sup>3</sup>	9.0	9.3					9.2	9.6						
dP <sup>4</sup>	9.6	10.4	8.9	8.9			9.5	10.5						
dP <sup>1-4</sup>	30.7 (ca.)		9.8	9.8			10.4	11.1						
M <sup>1</sup>	13.0	12.4							13.1	13.4				
M <sup>2</sup>											15.0	15.0	13.6	14.0
M <sup>3</sup>														
dP <sub>1</sub>					4.2?									
dP <sub>2</sub>					7.0	3.6								
dP <sub>3</sub>					9.6	5.0								
dP <sub>4</sub>					9.3	5.7								
dP <sub>1-4</sub>					29.6									
M <sub>1</sub>					10.3	5.7								

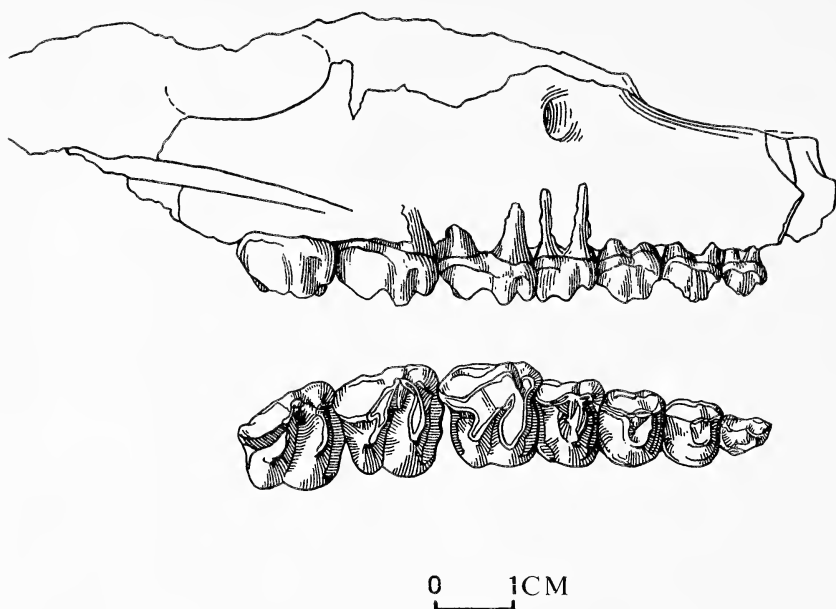


Fig. 37.—*Lophialetes expeditus*. Holotype, AMNH 19163.

slightly worn.  $dP_4$ : (only posterior part preserved) the angle between ectolophid and hypolophid  $90^\circ$ ; the position of hypoconulid somewhat prominent.  $M_1$ : anterior width almost the same as posterior width; metaconid distinct and convex anteriorly; a triangle-like process at the hypoconulid position.  $M_2$ : (only posterior part preserved) ectolophid and hypolophid developed; slight prominence at hypoconulid position.

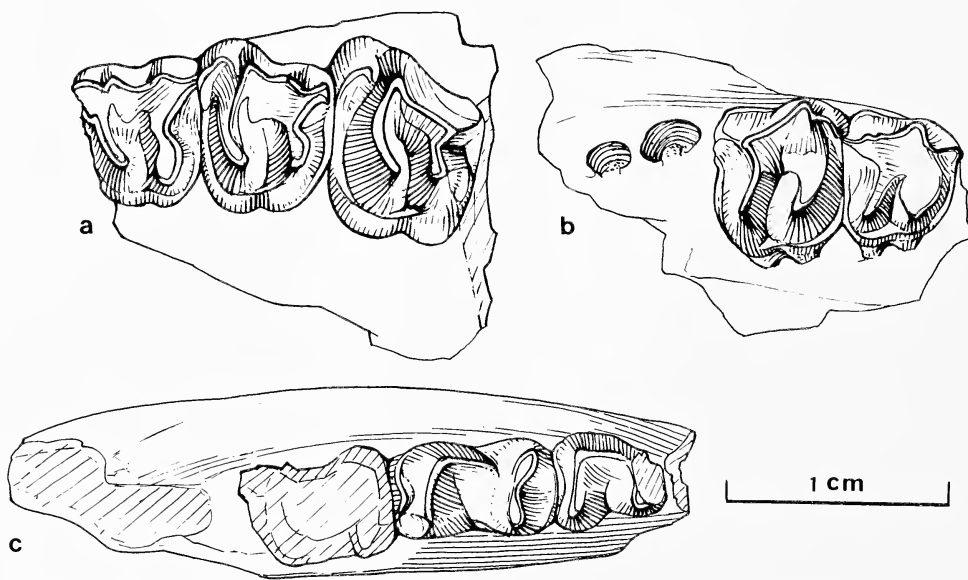
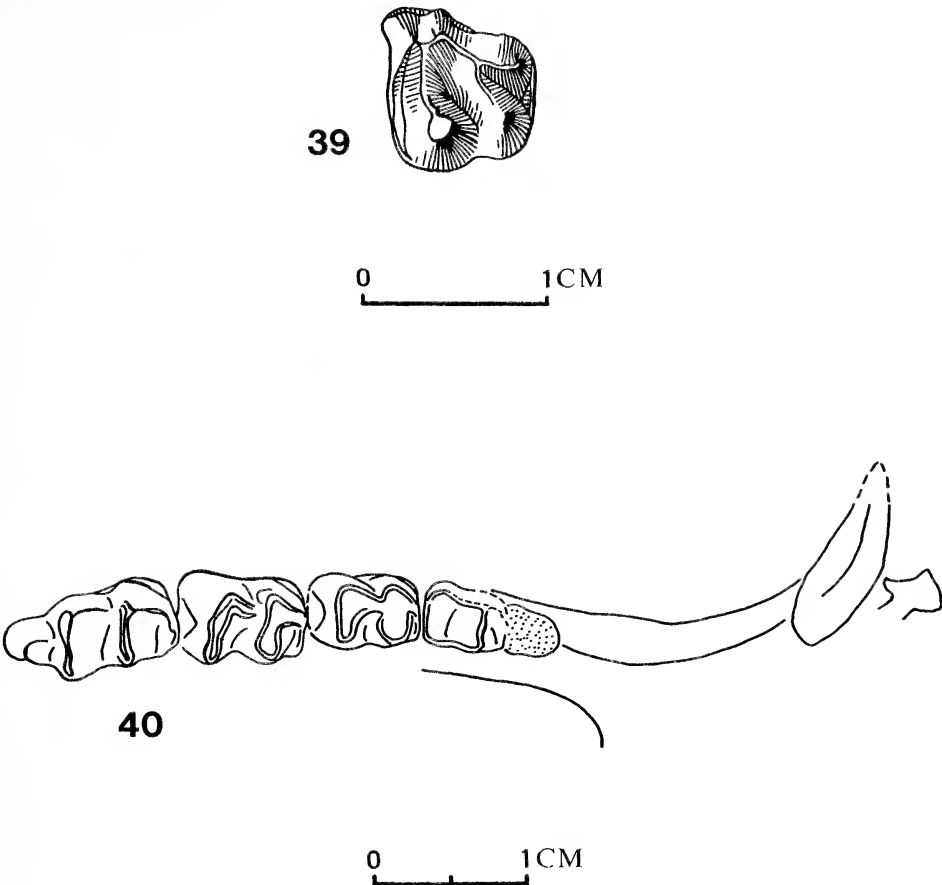


Fig. 38.—*Breviodon minutus*. (a) V5757,  $dP^{3-4}-M^1$ ; (b) V5758,  $dP^{3-4}$ ; (c) V5760,  $dP_4-M_1$ .



Figs. 39, 40.—*Breviodon minutus*. 39. Holotype, AMNH 20139 (from Matthew and Granger, 1925c, Fig. 8). 40. AMNH 26113, holotype of *B. acares*, left lower jaw with I<sub>3</sub> (reversed), C<sub>1</sub>, P<sub>3</sub> alveolus and P<sub>4</sub>–M<sub>3</sub>.

*Discussion.*—*Breviodon* was erected by Radinsky (1965, p. 203) and diagnosed as follows: “Very small lophialetids, with premolar series extremely short relative to molar series; P<sub>1-2</sub> lost. Symphysis broad, postcanine diastema long. Lower molar cusp patterns like those in *Lophialetes*.” He named a new species, *Breviodon acares*, and referred *Lophialetes minutus* with question to this genus as *Breviodon*?

Table 12.—Measurements (mm) of *Breviodon minutus*.

	V5757		V5758		V5759		V5760	
	L	W	L	W	L	W	L	W
dP <sub>3</sub>	5.8	6.3	5.4	5.5				
dP <sub>4</sub>	6.5	7.3						
M <sub>1</sub>	7.8	8.6						
dP <sub>4</sub>								3.9
M <sub>1</sub>					7.9?	5.0?		
M <sub>2</sub>					8.8	6.3		

*minutus*. According to the material (associated upper and lower cheek teeth) found in Mongolia, Reshetov (1975) considered *B. acares* to be a synonym of *Breviodon? minutus*, a conclusion followed here.

V5757 (dP<sup>3-4</sup> and M<sup>1</sup>) fit with V5759 (M<sub>1-2</sub>), so the two specimens are apparently associated. M<sup>1</sup> of V5757 fits with M<sup>1</sup> of *Breviodon minutus* (no. 3107-32) found in Mongolia, whereas the M<sub>1</sub> of V5759 is similar to that of "*Breviodon acares*" (AMNH 26113). This further confirms the synonymy of *B. minutus* and *B. acares*. On the anterior edge of dP<sup>3</sup> of V5757 there seems to be a wear facet, suggesting the presence of dP<sup>2</sup>.

Huang and Qi (1982) described a new species of *Breviodon*, *B. lumeiyiensis*, the teeth of which are similar to those of *B. minutus*, but smaller in size, the cheek teeth being twenty percent narrower than those of *B. minutus*.

Family Deperetellidae Radinsky, 1965  
*Teleolophus* Matthew and Granger, 1925  
*Teleolophus primarius*, new species  
 (Fig. 41; Table 13)

*Holotype*.—V5761, mandible with P<sub>2-4</sub> and M<sub>1-2</sub> (field no. 1P<sub>5</sub>H<sub>7</sub>).

*Referred specimens*.—V5762, mandible with M<sub>2-3</sub> (77027); V5763, 1-21: associated teeth, several carpi, and phalanges (including left P<sub>3</sub>, M<sub>1</sub>, and M<sub>2</sub> (77036-2); V5764, 1-2: two M<sub>1</sub> (77039); V5764, 1-2: two M<sub>1</sub> (1P<sub>5</sub>H<sub>8</sub>).

*Localities*.—Ulan Bulak, Huhe Bulak.

*Diagnosis*.—The metalophid is labial on P<sub>2</sub>, but not labial on P<sub>3</sub> and P<sub>4</sub>; premolars lacking entoconids; three pairs of incisors.

*Description*.—P<sub>2</sub>: metalophid near labial edge of crown; protoconid very close to metaconid; paraconid somewhat swollen; a rib-like crest on the internal wall of hypoconid; external cingulum relatively strong; internal cingulum incomplete. P<sub>3</sub>: protoconid and metaconid clearly separate; no hypolophid; a rib-like crest on the internal wall of hypoconid; trigonid longer than talonid. P<sub>4</sub>: paralophid short; trigonid relatively short; talonid longer than trigonid. M<sub>1</sub>: protolophid parallel to hypolophid; no metalophid; anterior cingulum weak; posterior cingulum very short. M<sub>2</sub>: paralophid very wide anteroposteriorly; anterior cingulum below the paralophid very weak; no metalophid; protolophid almost parallel to hypolophid. M<sub>3</sub> (V5762): similar to M<sub>2</sub> but posterior root curved posteriorly. Radiale (carpal bone): five facets, of which the facet that articulates with radius is the largest; two facets articulate with intermediate carpal, the distal of them narrow and long, and the proximal, wide and short; the other two facets are larger and articulate with the second and third carpal. Intermediate carpal bone: a total of seven facets—one flat facet articulates with the radius, two facets articulate with radiale (the proximal one is wide, the distal, narrow), two facets articulate with ulnar carpal(?), and the other two facets articulate with the third and fourth carpal bones. Fourth carpal bone: roughly triangular in proximal view; in distal view, wider anteriorly than posteriorly; seven facets for articulations—two with intermediate and ulnar carpal bones, three with third carpal bone and another two with third and fourth metacarpal. First phalanges: three different phalanges, under the second, third, and fourth metacarpals, respectively. Second phalanges: the one under second metacarpus is widest. Third phalanges: proximal surface with two facets; dorsal surface rough.

*Discussion*.—These specimens were found in adjacent sites, so the known distribution of this species is restricted. The main difference between *Teleolophus* and *Deperetella* is that the premolar series in the former is shorter than the molar series. Although P<sub>1</sub> and M<sub>3</sub> were not found on one specimen of *Teleolophus*, the length of P<sub>2-4</sub> is equivalent to M<sub>1-2</sub>. Therefore, the length of the P<sub>1-4</sub> must be shorter than M<sub>1-3</sub>.

The differences between *T. primarius* and *T. medius* (found in 1975, now under study) are as follows: 1) the three incisors are aligned anteroposteriorly in *T. primarius* but form a triangle in *T. medius*; the third incisor of *T. medius* is greatly reduced, and the canine is more robust; 2) the symphysis is narrower in *T. pri-*



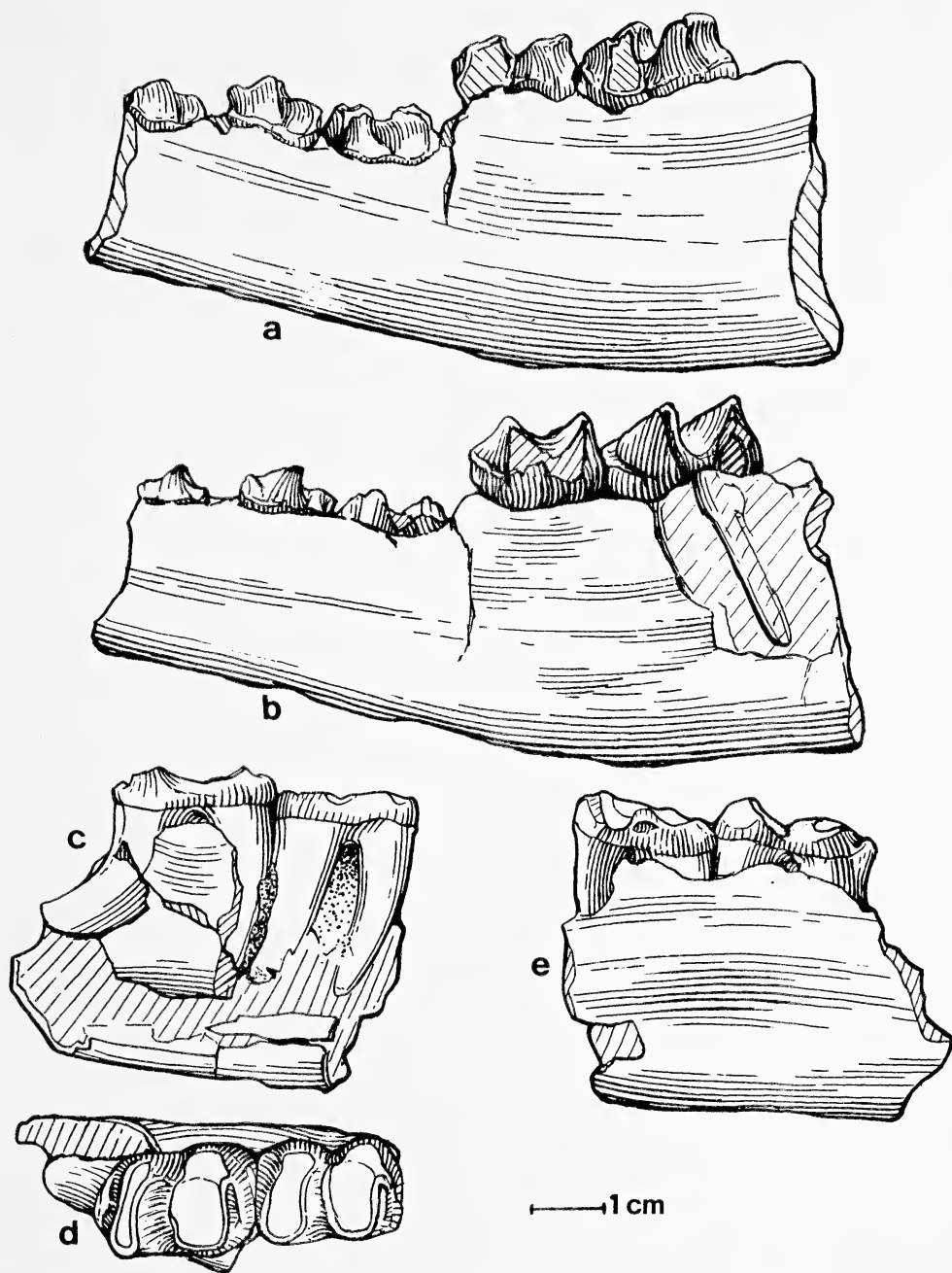


Fig. 41.—*Teleolophus primarius* new species. (a), (b) holotype, V5761, mandible with P<sub>2</sub>–M<sub>2</sub>, external and internal views; (c), (d), (e) V5762, mandible, with M<sub>2-3</sub>, internal, crown, and external views.



*marius*; 3) on  $P_2$  of *T. primarius* the metalophid is more labial, the metalophid is shorter, the entoconid is absent, and the protoconid and metaconid are not completely separated; 4)  $P_3$  is shorter and wider in *T. primarius* and there is an apparent notch separating the protolophid and metalophid, whereas this notch is absent in *T. medius*; a  $P_3$  entoconid is lacking in *T. primarius* but present in *T. medius*; 5)  $P_4$  is longer and wider in *T. primarius*, the notch between protolophid and metalophid is stronger, the paralophid is shorter and the metalophid longer; there is no entoconid, and a rib-like crest occurs on lingual wall of hypoconid; 6) the  $M_{1-2}$  paralophid is stronger in *T. primarius*; 7) the posterior root on  $M_3$  is curved posteriorly in *T. primarius* but is straight in *T. medius*.

These differences suggest the following phylogenetic trends in the genus *Teleolophus*: 1) reduction of incisors; 2) entoconid becoming prominent; 3) positions of metalophids of  $P_{2-3}$  becoming more labial; and 4)  $P_2$  protoconid gradually separating from metaconid.

***Teleolophus? rectus*, new species**  
(Fig. 42; Table 14)

*Holotype*.—V5766: two broken pieces of mandible with left  $P_4$  (anterior part broken) and  $M_1$ , and right  $P_4$  (posterior part broken),  $P_{2-3}$ , and  $M_2$  only roots left (field no. 1P<sub>5</sub>H<sub>8</sub>).

*Locality*.—Ulan Bulak.

*Diagnosis*.— $P_4$ : paralophid closer to lingual edge of crown, metalophid aligned almost with the medial part of the talonid; entoconid indistinct.

*Description*.— $P_4$ : paralophid short, originates from protolophid rather than protoconid, so trigonid very short; metalophid almost medial on talonid; entoconid indistinct; cingula very weak and no internal cingulum.  $M_1$ : paralophid relatively short; metalophid developed, not connected with protolophid.

*Discussion*.—The main characters of *Teleolophus rectus* are the position of the paralophid of  $P_4$ , which is closer to the lingual edge of the crown, the metalophid located almost medially on the talonid, and presence of a weak entoconid. In tooth morphology, *T. rectus* appears intermediate between *T. primarius* and *T. medius*.

Suborder Brontotherioidea Hay, 1902

Family Brontotheriidae Marsh, 1873

*Telmatherium* Marsh, 1872

*Telmatherium cristatum* (Granger and Gregory, 1943)

*Metatelmatherium cristatum* Granger and Gregory, 1943.

*Discussion*.—Granger and Gregory (1943, pp. 355–356) discovered that “the type skull of *Telmatherium ultimum* Osborn from the Uinta (upper Eocene) of North America so closely resembles the type of our *Metatelmatherium cristatum* in all aspects that one can barely discover specific differences between them . . .” Nevertheless, they erected a new genus, *Metatelmatherium*, from the Arshanto fauna, believing that it represented “a distinct generic stage characteristic of the upper Eocene of North America and Mongolia, a stage which is much larger and has more advanced premolars than the true *Telmatherium* . . .” The age of the Arshanto beds and Irдин Manha beds is now recognized as middle Eocene as is the North American Uintan. “*Metatelmatherium*” does not warrant recognition.

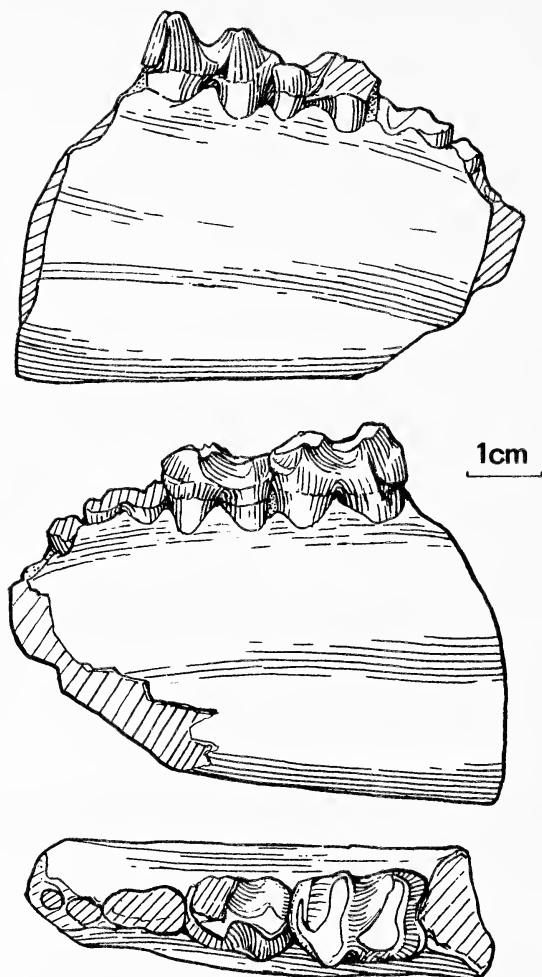


Fig. 42.—*Teleolophus? rectus* new species. Holotype, V5766 (in part), right mandible with left  $P_4$ – $M_1$ , external, internal, and crown views.

*Desmatotitan* Granger and Gregory, 1943

*Desmatotitan* sp.

(Fig. 43)

*Referred specimen.*—V5769: left  $M_3$  (field no. 77036-2).

*Locality.*—Huhe Bulak.

*Discussion.*—This tooth is wider and 10 mm longer than that of *Microtitan mongoliensis*, and is closer in size to that of *D. tukhumensis* (Ulan Shireh). V5769 also resembles that of *D. tukhumensis* in having relatively distinct cingula.

*Measurements.*—V5769,  $M_3$ , L/W: 58/28 mm.

*Protitan minor* Granger and Gregory, 1943

*Holotype.*—AMNH 26416. A skull, lacking the distal end of the nasals.

*Locality.*—Camp Margetts.

Table 14.—Measurements (mm) of *Teleolophus? rectus* (V5766).

	Left		Right	
	L	W	L	W
P <sub>2</sub>	9.7?			
P <sub>3</sub>	10.3?		9.9	
P <sub>4</sub>	13.2	10.3	13.6	10.0
M <sub>1</sub>	16.1	10.8	15.0?	
Depth of mandible below P <sub>4</sub> and M <sub>1</sub>	34.2		35.3	

*Discussion.*—Granger and Gregory (1943, pp. 358–359) erected this genus, which includes six species. Of them, only *Protitan minor* was collected from “probably top of Irдин Manha beds,” “Camp Margetts,” that is, from the top of what are here recognized as the Arshanto beds. Other species are probably based on materials from the Irдин Manha beds. Specific characters of *P. minor* are as follows (Granger and Gregory, 1943): “P<sup>1</sup> small, compressed; P<sup>2</sup> oblique, asymmetric, narrow; P<sup>3</sup> narrow; P<sup>4</sup> not nearly so wide as in *Epimanteoceras formosus*; M<sup>1</sup> of moderate width, M<sup>2</sup> narrow, M<sup>3</sup> fairly narrow; P<sup>4</sup> with slight tetartocone ridge but no cusp. Zygomata not wide. Basisphenoid pits conspicuous. Lower jaw not definitely known but the distance from the hypocone to the anterior rim of P<sup>2</sup> (217), which should be equal to the distance from the hypoconulid to the tip of P<sub>2</sub>, is nearly matched in a lower jaw, AMNH 26410, from the same locality and horizon. This jaw agrees well in other measurements and dental characters with the type skull and is therefore referred to this species. It differs from the type of *D. olseni* chiefly in its smaller dimensions but tends to confirm the reference of that form to *Protitan grangeri*. AMNH 20108, a maxilla, is close to *P. minor* in general, but the M<sup>3</sup> is much larger. The latter is in an early stage in lengthening, a process which was carried to an extreme in *Gnathotitan*.”

*Microtitan* Granger and Gregory, 1943

*Microtitan? elongatus*, new species

(Fig. 44)

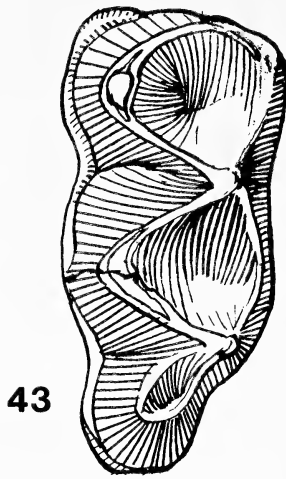
*Holotype.*—V5767, right P<sup>3</sup>–M<sup>3</sup> (M<sup>1</sup> and M<sup>2</sup> largely broken; M<sup>3</sup> preserves only mesostyle and metacone) (field no. 77028H<sub>2</sub>).

*Locality.*—Daatein Obo.

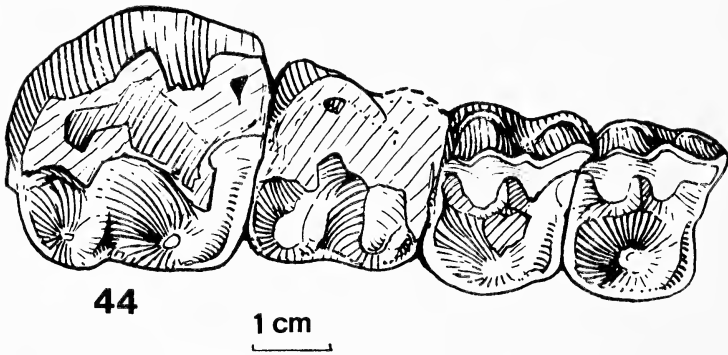
*Diagnosis.*—Larger than *Microtitan mongoliensis*; P<sup>3</sup> and P<sup>4</sup> wider than long (although width of P<sup>3</sup> is close to that of P<sup>4</sup>), mesostyles on P<sup>3</sup> and P<sup>4</sup> well developed and forming triangular processes on the external walls of the teeth, cingula developed.

*Description.*—P<sup>3</sup>: protocone prominent; paracone and metacone present; parastyle fairly well developed; mesostyle high, forming a triangular process on the external wall, which connects with prominent external cingulum; metastyle also fairly distinct; the base of the tooth rounded by a cingulum which separates from external cingulum at the parastyle and the metastyle. P<sup>4</sup>: similar to P<sup>3</sup>, but wider and parastyle more prominent. M<sup>1</sup>: (protocone and hypocone heavily worn) metacone well developed. M<sup>2</sup>: apparently larger than M<sup>1</sup>, with no wear on hypocone. M<sup>3</sup>: (only ectoloph preserved) the distance between paracone and mesostyle is smaller than that between mesostyle and metacone.

*Discussion.*—*Microtitan? elongatus* is slightly larger than *M. mongoliensis*. P<sup>3</sup> and P<sup>4</sup> of *Microtitan? elongatus* are wider than long and rectangular in crown view whereas P<sup>3–4</sup> are square in *M. mongoliensis*. The mesostyles on P<sup>3–4</sup> of *M.?*

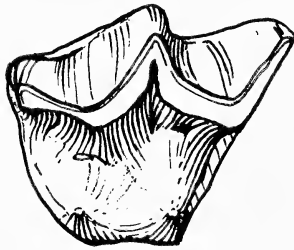


43



44

1 cm



45

Fig. 43.—*Desmatotitan* sp. V5769, right  $M_3$ .

Fig. 44.—*Microtitan?* *elongatus* new species. Holotype, V5767 (in part),  $P^3$ – $M^2$ .

Fig. 45.—*Microtitan* sp. V5768, right  $M^2$ .

*elongatus* and especially the triangular processes on the external wall are rarely seen in titanotheres and are absent in *M. mongoliensis*. On  $P^3$  and  $P^4$  of *Microtitan?* *elongatus* the basal cingula are more nearly continuous than in *M. mongoliensis*.

*Microtitan? elongatus* differs from *Protitan minor* (AMNH 26417) as follows:  $P^{3-4}$  are apparently smaller; widths of  $P^3$  and  $P^4$  are subequal ( $P^4$  is larger than  $P^3$  in *P. minor*);  $P^{3-4}$  protocones are more prominent; and the paracone is almost medial on the ectoloph whereas it is more anterior in *Protitan minor*.

*Measurements.*—L/W:  $P^3$ , 19.0/23.3 mm;  $P^4$ , 17.7/24.6 mm.

*Microtitan* sp.

(Fig. 45)

*Referred specimen.*—V5768, right  $M^2$  (field no. 77027).

*Locality.*—Huhe Bulak.

*Discussion.*—This tooth was found low in the Arshanto section along with *Microtitan elongatus*.

*Measurements.*—V5768,  $M^2$ , L/W: 37/29 mm.

Suborder Rhinocerotidea Gill, 1872

Family Hyracodontidae Cope, 1879

*Forstercooperia* Wood, 1939

***Forstercooperia huhebulakensis*, new species**

(Fig. 46; Table 15)

*Holotype.*—V5770, a broken skull with  $P^4$ – $M^3$  (field no. 77036-2).

*Referred specimen.*—V5771, a broken mandible with  $P_3$ – $M_3$  ( $M_3$  heavily broken) (77036-2); V5772,  $M_2$  and  $M_3$  (77036-2).

*Locality.*—Huhe Bulak.

*Diagnosis.*—Skull low; zygomatic arch long; upper cheek teeth similar to those of *Forstercooperia confluens*, but  $M^3$  with metacone; metalophids long and connect with protolophids. Differs from *F. totadentata* in its apparently smaller size and from *F. confluens* in having 1) zygomatic arch flatter and straighter; 2) in lateral view flatter frontal and nasal bones; 3)  $M^2$  and  $M^3$  without anti-crochets. Differs from *F. sharamurunensis* in having less molarized premolars.

*Description.*—Skull: frontal flat and low; zygomatic arch relatively flat and straight; anterior edge of orbit anterior to  $M^3$ ; sagittal crest well developed, parietal fairly high; interparietal very distinct; occipital crest thin; occipital part deeply convex forward; occipital condyle large; paramastoid process may be very robust; length of bulla, 27 mm.  $P^4$ : paraloph and metaloph form a semi-circle with wear; anterior and posterior cingula present; no internal nor external cingula.  $M^1$ : (heavily worn) paraloph fairly robust; metaloph more robust; paracone prominent forming a clear paracone rib; metacone relatively prominent, but metacone rib not present; angle between metaloph and metacone crest about 90°; anterior cingulum weak; no internal nor posterior cingula, external cingulum short, near ectoloph.  $M^2$ : larger in size; paraloph robust; dental wall with posteriorly projecting process at the position of the anti-crochet; paracone prominent; metacone rib fairly strong, the angle between metaloph and metacone (crest) about 90°; paraloph and metaloph connect at the base; anterior and posterior cingula weak.  $M^3$ : no anti-crochet; parastyle not prominent; paracone high; ectoloph connects with metaloph forming straight crest, but metacone very distinct; paraloph not connecting with metaloph at the base; anterior cingulum relatively strong.

Mandible: vertical edge fairly flat and straight; the angle between horizontal ramus and ascending ramus larger than 90°; foramen mentale clear.  $P_3$ : protoconid close to metaconid; protolophid long; metalophid fairly short; no cingulum.  $M_1$ : smaller than  $M_2$ ; protolophid parallel to hypolophid; metalophid not connecting with protolophid; no cingulum.  $M_2$ : similar to  $M^1$ , but with extremely weak cingulum on external wall.  $M_3$ : (heavily broken) metalophid connects with protolophid.

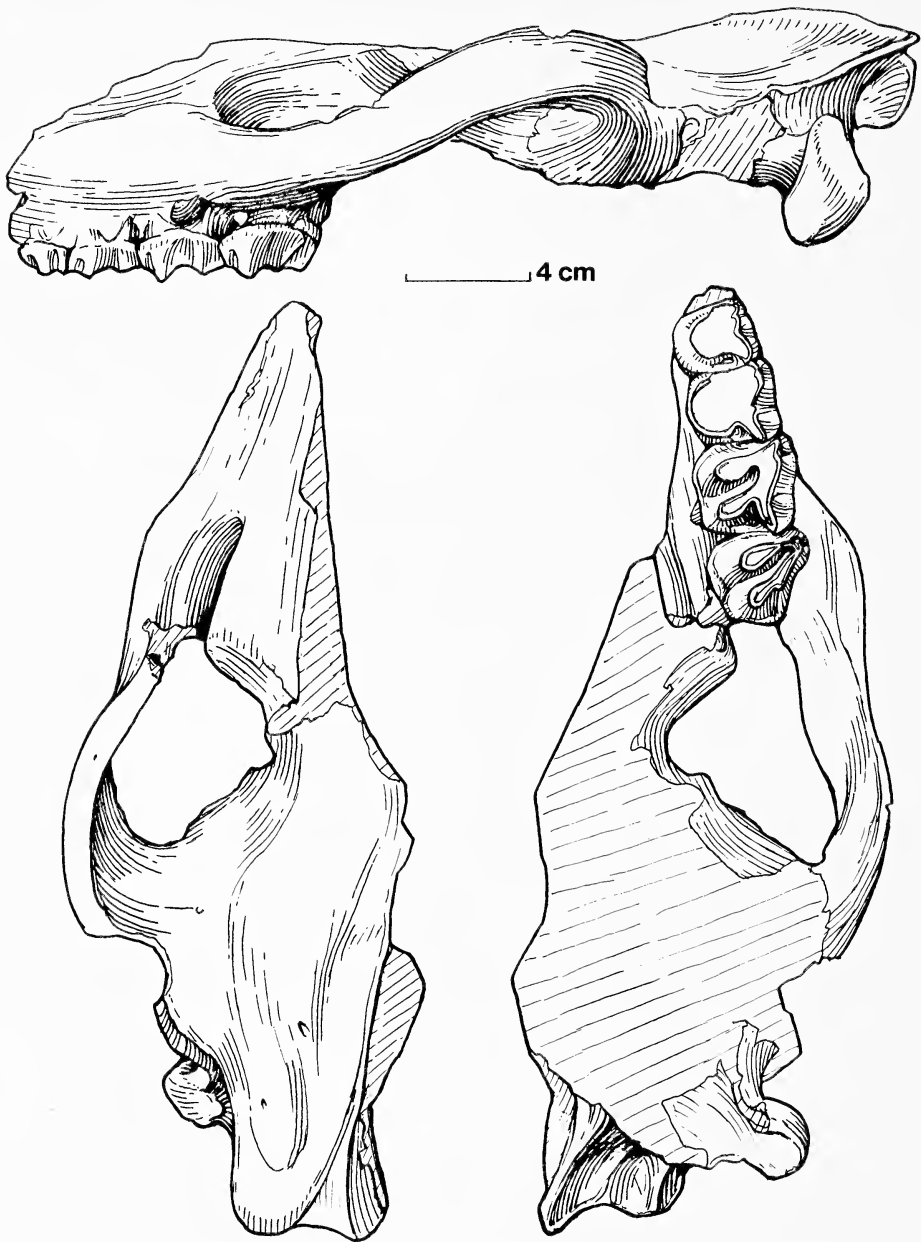


Fig. 46.—*Forstercooperia huhebulakensis* new species. Holotype, V5770, skull, lateral, dorsal, and palatal views.

*Discussion.*—The family Hyracodontidae has 11 genera, of which most are Eocene; *Ardynia*, *Urtinotherium*, and *Indricotherium* are Oligocene.

The shape of the upper cheek teeth agrees with *Forstercooperia*, especially  $P^4$  and  $M^3$ . The length of  $M^{1-3}$  of *F. huhebulakensis* is close to that of *F. confluens*



Table 15.—Measurements (mm) of *Forstercooperia huhebulakensis*.

	L	W
V5770		
P <sup>4</sup>	20.0	23.5
M <sup>1</sup>	24.5	27.5
M <sup>2</sup>	29.2	30.3
M <sup>3</sup>	26.0	30.0
M <sup>1-3</sup>	79.7	
Length, anterior edge of orbital fossa to condyle	213.0	
Width, across zygomatic arch	190.0	
Height, from lower border of condyle to occipital crest	93.0	
V5771		
P <sub>3</sub>	13.7	10.2
P <sub>4</sub>	16.0	12.9
M <sub>1</sub>	22.2	17.0
M <sub>2</sub>	26.3	17.7?
M <sub>3</sub>		17.0?
V5772		
M <sub>2</sub>	26.8	19.1
M <sub>3</sub>	29.8	18.0
Depth, mandible below M <sub>1</sub>	50.0	

(79.7 mm and 87.1–90.5 mm, respectively). *F. huhebulakensis* differs from species of *Hyracodon* in having the paracone higher than the ectoloph whereas in the latter the paracone is weak and not separated from the ectoloph. *F. huhebulakensis* differs from species of *Triplopus* in that the M<sup>3</sup> has a distinct metacone, and from species of *Allacerops* in being smaller.

*F. huhebulakensis* occurs stratigraphically lower than other species of this genus. Some phylogenetic trends within this genus (from *F. huhebulakensis* to *F. confluens* and *F. totadentata* to *F. sharamurunensis*) are: 1) increase in size; 2) nasal notch more posterior; 3) molarization of premolars. As Radinsky (1967*b*) suggested, *Forstercooperia* may be the ancestor of *Indricotherium*.

*Forstercooperia? grandis* (Peterson) 1919  
(Fig. 47a)

*Referred specimen*.—V5773, right P<sup>4</sup> (ectoloph missing).

*Discussion*.—The cingulum continuous on the internal side of the tooth; the paraloph is long, the protocone robust, metaloph short, and crista evident. This tooth is larger than P<sup>4</sup> of *F. huhebulakensis*, and resembles that of North American *Forstercooperia? grandis* (UCMP 69722). The metaloph of the North American form is not continuous nor is it in the Inner Mongolian specimen after wear. In dimensions this tooth is close to P<sup>4</sup> of *F. totadentata*, but the latter lacks a continuous cingulum and crista.

*Measurements*.—V5773, P<sup>4</sup>, L/W: 19.4/22.1 mm (ca.).

*Forstercooperia* sp.  
(Fig. 47b, c)

*Referred specimens*.—V5777, left M<sup>3</sup> (field no. 77028H<sub>2</sub>); V5774, right M<sub>2</sub> (77028H<sub>2</sub>).

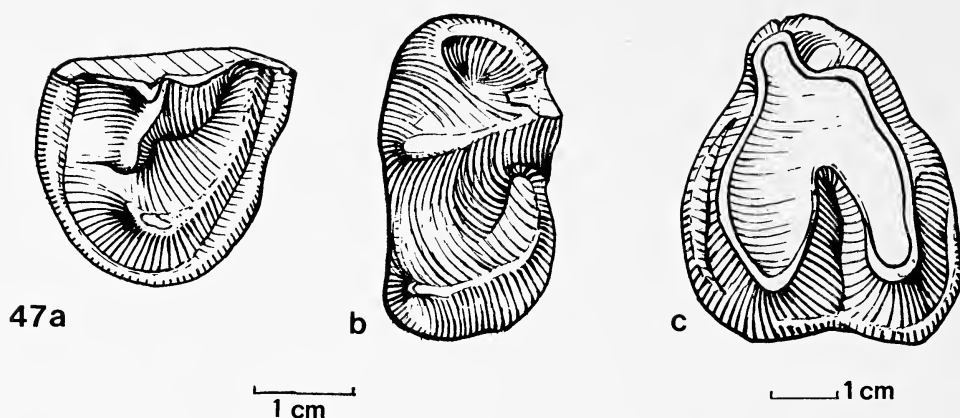


Fig. 47a-c.—*Forstercooperia?* *grandis*. V5773, right P<sup>4</sup>. b, c.—*Forstercooperia* sp. (b) V5774, right M<sub>2</sub>; (c) V5777, M<sup>3</sup>.

*Locality*.—Daatein Obo.

*Discussion*.—In regard to the dental pattern, M<sup>3</sup> (V5777) is quite similar to M<sup>3</sup> of *Urtinotherium incisivum*, but the dimensions are too different between the two M<sup>3</sup>s. Besides this, V5777 has a small cingulum while *Urtinotherium incisivum* lacks one. The discovery of this tooth provides some clue to the phylogeny of the Hyracodontidae. The length of V5774 (M<sub>2</sub>) is close to that of *Forstercooperia confluens* but its width is less. The width of the protolophid is larger than that of metalophid, a phenomenon rarely seen in the family Hyracodontidae.

*Measurements*.—L/W: M<sup>3</sup> (V5777), 40.0/46.5 mm.

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## Appendix 1.—List of Irdin Manha fauna.

	Irdin Manha	Ulan Shireh	Huhe Bulak (Camp Margetts)	Lushi (Henan)	Mon- golia
Order Primates					
Anaptomorphidae					
<i>Lushius qinlinensis</i>				X	
Order Insectivora					
? <i>Pantolestes</i> sp.	X				
Order Rodentia					
Paramyidae					
paramyid spp.	X				
Cocomyidae					
<i>Tsinlingomys youngi</i>				X	
Yuomyidae					
<i>Advenimus bohlini</i>		X			
cf. <i>Advenimus</i> sp.		X			
<i>Yuomys weijingensis</i>		X			
Order Lagomorpha					
Leporidae					
<i>Shamolagus grangeri</i>		X			
<i>Lushilagus lohoensis</i>				X	
Order Creodonta					
Oxyaenidae					
<i>Sarkastodon mongoliensis</i>	X	X			
Hyaenodontidae					
<i>Paracynohyaenodon morrisoni</i>	X				
<i>Propterodon irdinensis</i>	X				
<i>Hyaenodon</i> sp.				X	
Order Carnivora					
Miacidae					
<i>Miacis invictus</i>	X				
<i>M. lushiensis</i>				X	
miacid indet.		X			
Canidae					
<i>Cynodictis</i> sp.				X	
Felidae					
cf. <i>Eusmilus</i> sp.				X	
Order Acreodi					
Mesonychidae					
<i>Andrewsarchus mongoliensis</i>	X				
<i>A. henanensis</i>				X	
<i>A. gigas</i>			X	X	
<i>Hapalodectes serus</i>	X				
? <i>Hapalodectes serus</i>		X			
? <i>Harpagolestes orientalis</i>		X			
<i>Honanodon macrodontus</i>				X	
<i>Lohodon lushiensis</i>				X	
<i>Pachyaena</i> sp.	X				
<i>Mesonyx</i> sp.	X	X			
mesonychid indet.	X	X			

## Appendix 1.—Continued.

	Irdin Manha	Ulan Shireh	Hube Bulak (Camp Margetts)	Lushi (Henan)	Mon- golia
Order Tillodontia					
Stylinodontidae					
?Stylinodon sp.				X	
Order Pantodonta					
Coryphodontidae					
<i>Eudinoceras mongoliensis</i>	X	X			X
<i>E. kolobolchiensis</i>					X
<i>Eudinoceras</i> sp.				X	
<i>Hpercoryphodon thomsoni</i>			X		
Pantolambdodontidae					
<i>Pantolambdodon inermis</i>		X			
<i>P. fortis</i>		X			
Order Perissodactyla					
Brontotheriidae					
<i>Telmatherium parvum</i>	X				
<i>Protitan grangeri</i>	X			X	
<i>P. robustus</i>	X				
<i>P. obliquidens</i>	X				
<i>P. bellus</i>		X			
<i>Rhinotitan grangeri</i>				X	
<i>Microtitan mongoliensis</i>	X	X			
?Microtitan sp.				X	
<i>Desmatotitan tukhumensis</i>		X			
<i>Epimanteoceras formosus</i>		X			
<i>Dolichorhinoides augustidens</i>		X			
<i>Acrotitan ulanshirehensis</i>		X			
brontotheriid indet.			X		
Eomoropidae					
<i>Lunania youngi</i>				X	
<i>Eomoropus</i> sp.				X	
Isectolophidae					
isectolophid indet.					X
Helaletidae					
<i>Helaletes mongoliensis</i>	X				
?Colodon sp.				X	
Lophialetidae					
<i>Lophialetes expeditus</i>	X	X	X		
<i>Lophialetes</i> sp.	X	X			
<i>Breviodon minutus</i>	X	X		X	X
?Breviodon minutus					X
cf. <i>Breviodon minutus</i>		X			
?Breviodon sp.		X			
<i>Parabreviodon dubius</i> (=cf. <i>Brevio-</i> <i>don acares</i> , Radinsky, 1965, prob- ably Irdin Manha beds.)	X				
<i>Simplaletes sujiensis</i>	X	X			
<i>S. ulanshirehensis</i>		X			
<i>Zhongjianoletes chowi</i>		X			
<i>Zhongjianoletes</i> sp.		X			
<i>Pataecops parvus</i>					X

Appendix 1.—Continued.

	Irdin Manha	Ulan Shireh	Huhe Bulak (Camp Margetts)	Lushi (Henan)	Mon- golia
Deperetellidae					
<i>Teleolophus medius</i>	X	X			X
<i>Deperetella</i> sp.				X	
Hyracodontidae					
<i>Rhodopagus pygmaeus</i>	X	X			
<i>Rhodopagus</i> sp.					X
? <i>Triplopus proficiens</i>	X	X			
<i>Triplopus</i> sp. (= <i>Caenolophus</i> or Amyndontidae)				X	
<i>Forstercooperia totadentata</i>	X				
<i>Forstercooperia</i> cf. <i>grandis</i>		X			
<i>Forstercooperia</i> spp.				X	
<i>Teilhardia pretiosa</i> ("Ulan Shireh" beds)		X			
<i>Prohyracodon</i> sp.				X	
Amynodontidae					
<i>Lushiamynodon menchiapuensis</i>				X	
? <i>Lushiamynodon sharamurunensis</i>		X			
<i>Sianodon honanensis</i>				X	
Order Artiodactyla					
Dichobunidae					
<i>Dichobune</i> sp.				X	
Choeropotamidae					
<i>Gobiohyus orientalis</i>	X	X?		X	
<i>G. pressidens</i>	X				
<i>G. robustus</i>	X			X	
Cebochoeridae					
achaenodont indet.	X				
Anthracotheriidae					
<i>Anthracotherium</i> spp.				X	
Leptomerycidae					
cf. <i>Archaeomeryx</i> indet.	X				
Order indet.					
Didymoconidae					
<i>Mongoloryctes auctus</i>	X				
<i>Kennatherium shirehensis</i>		X			

## Appendix 2.—Middle Eocene mammals in the central part of Shandong Province.

	Xintai	Mengyin	Laiwu
Order Condylarthra			
Hyopsodontidae			
? <i>Haplomylus</i> sp.		X	
Order Tillodontia			
Esthonychidae			
<i>Kuanchuanius shangtungensis</i>	X		
Order Pantodonta			
Coryphodontidae			
<i>Coryphodon flerowi</i>	X		
<i>Metacoryphodon xitaiensis</i>	X		
Order Dinocerata			
Uintatheriidae			
cf. <i>Uintatherium</i> ? sp.	X		
Order Rodentia indet.	X		
Order Creodonta			
Hyaenodontidae			
<i>Thinocyon? sichowensis</i>	X		
Order Perissodactyla			
Equidae			
<i>Propalaeotherium sinense</i>		X	
<i>Propalaeotherium</i> sp.	X		
(Hyracotheriinae: two species, no names, Zdansky, 1930)		X	
Brontotheriidae			
gen. and sp. indet.	X		
Chalicotheriidae			
<i>Grangeria canina</i>	X		
Helaletidae			
<i>Hyrachyus modestus</i>			X
<i>H. modestus</i> ?	X		
<i>H. metalophus</i>	X		
<i>Helaletes</i> sp.	X		
Lophialetidae			
<i>Lophialetes</i> sp.	X		
<i>Schlosseria</i> sp.	X		
<i>Breviodon? minutus</i>	X		
Deperetellidae			
<i>Teleolophus shandongensis</i>	X		
<i>Teleolophus</i> sp.	X		
Hyracodontidae			
<i>Rhodopagus laiwuensis</i>			X
<i>Rhodopagus</i> sp.	X		
Order indet.			
<i>Heptaconodon dubium</i>		X	



Appendix 3.—Middle Eocene mammals in Zaisan Basin, Kazakhstan, U.S.S.R.

	Aksyir	Tschai- bulak	Obaila	Kalmak- pay	Ulken- Ulasty
Order Rodentia					
Cocomyidae					
<i>Tamquammys tantillus</i>	X	X			X
Yuomyidae					
<i>Saykanomys chalchas</i>	X				X
<i>Petrokozlovina notas</i>	X				
Order Lagomorpha					
Leporidae					
<i>Shamolagus</i> sp.	X				
Order Condylarthra indet.		X			
Order Creodonta					
Hyaenodontidae					
cf. <i>Limnocyoninae</i>					X
deltatheriid indet.					X
Order Pantodonta					
Coryphodontidae					
<i>Eudinoceras obailensis</i>			X	X	
pantodont indet.					X
Order Perissodactyla					
Brontotheriidae					
<i>Palaeosyops</i> sp.	X				
Isectolophidae					
<i>Isectolophus bogdulensis</i>			X		
cf. <i>Isectolophus</i> sp.		X			
Helaletidae					
<i>Veragromovia desmatotheroides</i>			X		
<i>Helaletes</i> cf. <i>mongoliensis</i>			X		
<i>Helaletes</i> sp.	X				
helaletid indet.					X
Lophialetidae					
<i>Lophialetes</i> cf. <i>expeditus</i>				X	
<i>Lophialetes minor</i>				X	
<i>Lophialetes</i> n. sp.		X			
<i>Breviodon</i> sp.	X				
lophialetid indet.		X			
Deperetellidae					
<i>Teleolophus</i> cf. <i>medius</i>			X		
deperetellid indet.					X
Hyracodontidae					
<i>Rhodopagus</i> cf. <i>pygmaeus</i>		X			
<i>Triplopus</i> cf. <i>implicatus</i>			X	X	
<i>Triplopus</i> sp.		X	X	X	
cf. <i>Triplopus</i> sp.	X				
<i>Prohyracodon</i> sp.	X				
hyracodontid indet.				X	
Order Artiodactyla					
Dichobunidae					
dichobunid indet.	X				
Order uncertain					
<i>Paraphenocodus solivagus</i>	X				
<i>Aksyiria oligestus</i>	X				

Appendix 4.—*Middle Eocene mammals from Pakistan and India.*

	Ganda Kas	Kalakot	Chor- lakkhi	Kutch	Kohat
Order Insectivora indet.			X		
Order Chiroptera indet.			X		
Order Primates					
Adapidae indet.			X		
Order Condylarthra(?)					
Hyopsodontidae(?)					
<i>Dulcidon gandaensis</i>	X				
Order Acreodi					
Mesonychidae					
cf. <i>Honanodon</i>		X			
indet.	X				
Order Tillodontia					
<i>Basalina basalensis</i>	X		X		
Order Cetacea					
Protocetidae					
<i>Pakicetus inachus</i>					X
<i>Gandakasia potens</i>	X		X		
<i>Protocetus sloani</i>				X	
<i>P. horudiensis</i>				X	
<i>P. attoki</i>	X				
indet.	X				
<i>Indocetus ramani</i>				X	
<i>Ichthyolestes pinfoldi</i>	X		X		
Agorophiidae					
<i>Andrewsiphium kutchensis</i>				X	
<i>A. minor</i>				X	
Order Creodonta					
Hyaenodontidae					
<i>Paratritemnodon indicus</i>	X	X	X		
Order Carnivora					
Miacidae indet.			X		
Order Sirenia					
Protosirenidae					
<i>Protosiren fraasi</i>				X	
Order Proboscidea					
Anthracobunidae					
<i>Lammidhania wardi</i>	X				
<i>Jozaria palustris</i> (Kohat District)					X
<i>Anthracobune pinfoldi</i>	X	X		X	
<i>A. pilgrimi</i>	X				
Order Perissodactyla					
Hyracodontidae					
<i>Prothyraodon</i> (?) <i>kalakotensis</i>		X			
<i>Forstercooperia jigniensis</i>		X			
Isectolophidae					
<i>Sastrilophus dehmi</i>		X			

## Appendix 4.—Continued.

	Ganda Kas	Kalakot	Chor- lakki	Kutch	Kohat
<b>Heleatidae</b>					
<i>Hyrachyus asiaticus</i>		X			
<i>H. (Chasmothereium) mckennai</i>		X			
<b>Deperetellidae</b>					
<i>Teleolophus(?) daviesi</i>	X				
<b>Lophialetidae</b>					
<i>Schlosseria radinskyi</i>		X			
<i>Kalakotia simplicidentata</i>	X				
<i>Aulaxolophus quadrangularis</i>		X			
<b>Brontotheriidae</b>					
<i>Eotitanops dayi</i>	X				
<i>Pakotitanops latidentatus</i>	X				
<b>Order Artiodactyla</b>					
<b>Helohyidae</b>					
<i>Khirtharia dayi</i>	X	X	X		
<i>Gobiohyus orientalis</i>	X				
<b>Dichobunidae</b>					
<i>Kunmunella rajauriensis</i>		X			
<i>Chorlakkia hassani</i>			X		
<b>Choeropotamidae</b>					
<i>Indohyus(?) kalakotensis</i>		X			
<i>Indohyus indirae</i>		X	X		
<b>Raoellidae</b>					
<i>Raoella dograi</i>		X			
<i>Anthracokeryx</i> sp.	X				
<i>Haqueina haquei</i>	X				
<b>Order Rodentia</b>					
<b>Cocomyidae</b>					
<i>Tamquammys</i> sp.				X	
<b>Chapattimyidae</b>					
<i>Saykanomys ijlsti</i>	X				
<i>S. chalchae</i>	X	X			
<i>S. vandermueleni</i>	X				
<i>S. sondaari</i>	X				
<i>S. lavocati</i>	X				
<i>Chapattimys ibrahimshahi</i>	X				
<i>C. wilsoni</i>	X				
<i>Petrokoslovia</i> sp.				X	
<i>Metkamys blacki</i>		X			



ECOLOGY OF SMALL MAMMALS IN A GALLERY  
FOREST OF CENTRAL BRAZILLESLIE ZUHN NITIKMAN<sup>1</sup>MICHAEL A. MARES<sup>2</sup>

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## ABSTRACT

A 7-month mark-recapture study of small mammals was conducted on a 1-ha plot in a gallery forest associated with the Cerrado grasslands of central Brazil. The natural history of small mammals in these forests is poorly known. Ten species were caught: two marsupials (*Monodelphis americana* and *Marmosa agilis*) and eight rodents (*Oryzomys bicolor*, *O. capito*, *O. concolor*, *O. nigripes*, *Rhipidomys mastacalis*, *Akodon cursor*, *Bolomys lasiurus*, and *Oxymycterus roberti*). The present study provides information on a number of life-history characteristics (body size, sex ratios, age class ratio, biomass estimates, survivorship estimates, movement patterns, and habitat utilization patterns). *M. agilis* was the most commonly captured arboreal species (192 times), and *B. lasiurus* was the most frequently caught terrestrial species (141 times). *M. agilis* had the longest mean residency (56.1 days), as well as the highest mean number of captures per marked individual (12.0 times). *O. bicolor* traveled the greatest mean distance between successive captures (45.2 m). *O. concolor* males moved 45.3 m between consecutive captures, much further than female conspecifics (25.9 m). Movement patterns were analyzed for the six most common species (*M. americana*, *M. agilis*, *O. capito*, *O. concolor*, *O. nigripes*, *A. cursor*, and *B. lasiurus*); all exhibited nonrandom movement through the study area. Habitat variables were analyzed by principal component and cluster analyses in order to evaluate habitat preferences with respect to six distinct microhabitats: three types of semideciduous gallery forest (dense forest, vine tangle forest, and forest mosaic), two types of forest ecotones (forest edge and bamboo edge), and one disturbed area (fern thicket). *A. cursor* frequented the dense forest, whereas *O. capito* was caught primarily in dense forest and forest mosaic. *B. lasiurus* was captured almost exclusively in the two ecotonal microhabitats. *O. concolor* had an apparent preference for the fern thicket. *O. nigripes* was trapped more frequently in fern thicket and dense forest than was expected. *M. agilis* tended to avoid the fern thicket, but ranged randomly throughout all other microhabitats.

## INTRODUCTION

The Cerrado is an endemic tropical savanna complex located in the highlands of central Brazil. The Cerrado exceeds 1.8 million km<sup>2</sup> in area (Ab'Sáber, 1971), occupying approximately 25% of Brazil's land area (Joly, 1970). It ranges from the northern part of the state of Goiás southward to western Minas Gerais state and from the western edge of the state of Bahia westward to eastern Mato Grosso and Rondônia states (Eiten, 1972). It is bordered by the Amazon rainforest to the north, semiarid Caatinga to the northwest, Atlantic Rainforest to the east, semiarid Chaco to the south, and Pantanal swamplands to the west.

The Cerrado is composed of four major habitats: cerrado sensu stricto (s.s.), cerradão, gallery forest, and campo (Eiten, 1972). The cerrado (s.s.) is the dominant habitat in the Cerrado vegetation complex. It is a sclerophyllous scrub woodland

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and is readily identified by its open canopy and twisted tree trunks and limbs. The *cerradão*, literally "big cerrado," is a taller, more dense scrub, practically a forest. The canopy is mostly closed and the trees are usually greater than 10 m in height. The gallery forest is a narrow band of vegetation, varying from a few meters to about 200 m in width, that occurs along permanent rivers and streams throughout the Cerrado; it is composed primarily of evergreen tree species. The gallery forest transition into savanna is abrupt; often the ecotone is no more than 5 m in width. Campo is a grassland that varies widely in structure from savannas with scattered low trees or shrubs (*campo cerrado*), to those with few but conspicuous shrubs (*campo sujo*), to prairies with essentially no woody plants (*campo limpo*). Floristically, the Cerrado region is the richest and most diverse savanna system in the world (Sarmiento, 1983). Heringer (1971) counted more than 300 plant species in 1 ha of cerrado (s.s.) in Distrito Federal. Heringer et al. (1977) listed 1063 vascular plant species for the entire Cerrado region and this list is not complete.

The gallery forest is one of the least-known habitats of the Cerrado. Floristically, the Cerrado in general is relatively well known, but only a few botanists have surveyed the gallery forest near Brasília (Barbosa et al., 1984; Ratter, 1980; I. Schiavini da Silva, personal communication). These preliminary studies suggest that gallery forests are very complex; neighboring forests can be markedly different in composition and form (Eiten, 1984). The gallery forest biota is diverse and shares a close affinity in terms of mammal species composition with the neighboring forests of the Amazon and the Atlantic Coast (Redford and Fonseca, in press). Although few, if any, mammals are endemic to gallery forests, many species range into central Brazil only via these mesic forest corridors (Alho, 1982; Redford and Fonseca, in press). To these forest mammals, the gallery forest is an extension of the Amazon or Atlantic rain forests, permitting them to range deeply into the Cerrado (Fonseca and Redford, 1984).

In spite of the great biotic diversity of the Cerrado, ecological studies of mammals are rare. Several recent investigations have provided valuable information on the ecology of various mammal species (e.g., Alho, 1979, 1981; Alho and Souza, 1982; Almeida et al., 1981; Borchert and Hansen, 1983; Dietz, 1981; Lacher et al., 1984; Mello, 1980; Paula, 1983; Pereira, 1982; Pereira and Alho, 1982; Redford, 1984; Souza, 1979; Souza and Alho, 1980). But even so, these studies represent relatively short-term efforts. Basic information on more species is required for advancements in theoretical work, such as analyses of ecosystems or patterns of adaptive radiation and speciation.

The objective of this study was to examine the ecology and natural history of small mammals in a Cerrado gallery forest. A small mammal community was studied using mark-recapture procedures over a 7-month period in 1984. In addition, data were obtained on climate and habitat structure.

#### STUDY SITE

The study site was located in a gallery forest on the Fazenda Água Limpa, a research and teaching field station jointly administered since the early 1960s by the Departamento de Agronomia and the Laboratório de Ecologia of the Universidade de Brasília. The field station (15°58'S, 47°57'W) encompasses 4062 ha and is located approximately 20 km SSW of downtown Brasília, Distrito Federal. The elevation is approximately 1000 m above sea level. Climatically, the region has a pronounced tropical wet and dry season, with the annual rainfall averaging 1526

mm (Eiten, 1984). The dry season lasts from three to four months during the Southern Hemispheric winter, during which the mean monthly rainfall is only 10.5 mm (Eiten, 1984). On average, 85% of the rain falls in a 6-month period from October to March. The mean daily temperature fluctuates little during the year. Based on a 20-year average for Brasília (1961–80), the mean seasonal temperature is 18.3°C in the two coldest months (June, July) and 21.5°C in the two warmest months (September, October) (Eiten, 1984).

Cerrado (s.s.) is the dominant vegetation type of Fazenda Água Limpa. Campo limpo also covers considerable area, including the higher ground towards the eastern boundary of the reserve. Cerradão is relatively rare within the reserve. Gallery forest occurs along the two permanent watercourses that run through the reserve (Capetinga Creek and Água da Onça). Both creeks eventually flow into Gama Creek, which in turn empties into Lake Paranoá in Brasília. The vegetation of Fazenda Água Limpa is discussed in more detail by Ratter (1980).

The 1-ha trapping grid was set in the Capetinga gallery forest, on the west side of the creek, approximately 3.5 km upstream from its confluence with Gama Creek. The grid was situated on a terrace that ranged from 2.5 to 10.0 m above the creekbed. The eastern edge of the grid ran along Capetinga Creek; whereas, the western edge was bounded by campo limpo habitat (Fig. 1). The Capetinga gallery forest showed evidence of human disturbance—there was some selective cutting of trees both during the study and in recent years. An overgrown network of trails still remained.

## MATERIALS AND METHODS

### *Field Techniques*

*Trapping.*—A 1-ha grid was established with 100 stations set at approximately 10-m intervals. The grid was irregularly shaped in order to fit the contours of the gallery forest (Fig. 1). Two collapsible Sherman traps (16 by 5 by 5 cm) were set at each station; one on the ground, next to low vegetation or alongside fallen trees, within a 1-m radius of the stake; the other in trees or vines up to 3 m off the ground and within a 2.5-m radius of the stake.

Trapping of small mammals was conducted from January through July 1984 (Table 1). There were seven trapping periods, roughly corresponding to each of the months. Trapping occurred 10 days/period during the first 5 months. In June, the trapping session was terminated after day 7; in July, traps were set for 11 days. During January, only 57 stations were used and only arboreal traps were set. A total of 12,170 trap-nights was completed on the grid—5800 trap-nights using ground traps and 6370 trap-nights using arboreal traps.

Live traps were baited with peanut butter, either plain or mixed with rolled oats. Traps were rebaited every two or three days as needed. When the minimum nighttime temperature was low enough to affect trap survivorship, cotton was added as insulating material. Animals trapped overnight were removed each morning. On several occasions, traps were checked in late afternoon to determine diurnal activity. Captured animals were marked by toe-clipping and examined to determine approximate age, and reproductive condition. They were then released immediately at the point of capture. Animals were weighed on the initial capture of each trapping period.

Voucher specimens (skin and skeleton) were prepared. They have been deposited in the collection at the Laboratório de Ecologia Animal, Universidade de Brasília and the Stovall Museum of Science and History, University of Oklahoma.

### *Data Analysis*

*Characterization of the habitat.*—Microhabitats were defined using cluster and principal components analyses on 26 habitat variables. Thirteen variables were direct measurements from each of the 100 trapping stations on the grid (Table 2). Most variables are self-explanatory. Density of trees was calculated as follows. At each station, a pair of trees (with DBH  $\geq 9$  cm) was marked within a 5-m radius of the stake at each station. The closest tree to the stake was selected as the "A" tree of the pair. The "B" tree was chosen as the one closest to the "A" tree. In all, 174 trees were marked. In

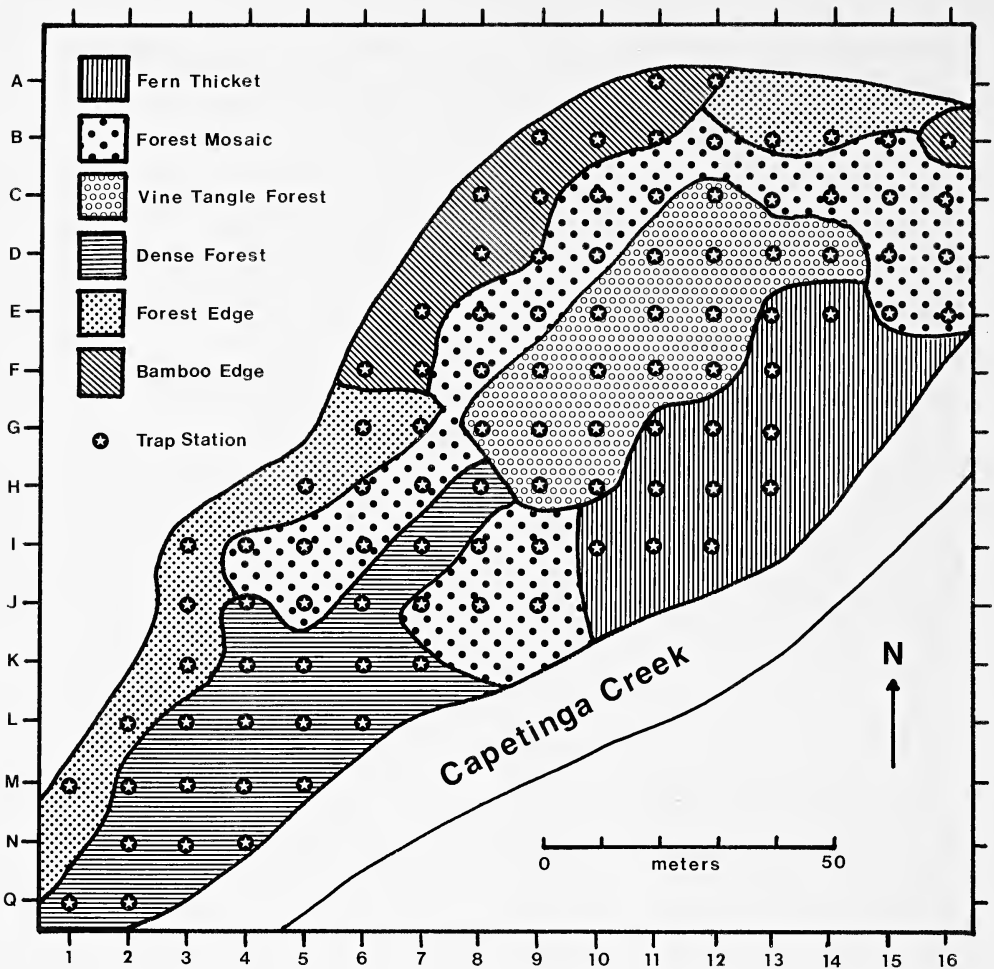


Fig. 1.—Map of the Capetinga study area.

order to include variables that described the area that surrounds each station, 13 more variables were calculated. These were the mean values for each of the original variables of the stations immediately surrounding each station. The number of adjacent stations included in these calculations varied from 1 to 4, depending on the position of the station on the grid. Raw data were standardized (i.e., to make the character mean 0 and the variance 1), and a dendrogram was constructed using the unweighted pair-group method using arithmetic averages (UPGMA; Sneath and Sokal, 1973) on an average distance matrix. Many of these variables were correlated; thus, a principal components analysis was performed on standardized data to produce a new set of orthogonal components to summarize the character variance. Trap sites were projected onto the resulting components using the standardized data.

Computations were performed on the IBM System 3081 and an Apple II at the University of Oklahoma. Most of the analyses were done using the following computer packages: BIOM (Rohlf, 1982); NT-SYS (Rohlf et al., 1979); and SAS (Barr et al., 1979).

*Species accounts.*—Only species with a sufficient number of captures were included in analyses requiring statistical testing. Animals captured initially as subadults and recaptured later as adults were included in both age class categories for analyses that compared the two classes. Age classes were estimated using pelage, genital characteristics, and mass.

Population size was estimated by direct enumeration, based on the minimum number of individuals



Table 1.—*Dates of trapping periods and numbers of traps used at Capetinga.*

Period	Dates	Duration (in days)	No. traps		Total trap-nights
			Arboreal	Ground	
1	11–20 Jan	10	56	—	560
2	23 Feb–3 Mar	10	100	100	2000
3	20–29 Mar	10	100	100	2000
4	19–28 Apr	10	100	100	2000
5	13–22 May	10	100	100	2000
6	15–21 Jun	7	100	100	1400
7	14–24 Jul	11	100	100	2200

known to be alive during a particular trapping period. Biomass, defined as the combined mass (in grams) of conspecifics per hectare, was used as a measure of ecological dominance. Monthly biomass estimates for each species were determined by multiplying the minimum number of individuals known alive each month by the mean monthly mass of all animals captured.

Sex ratio and age class distributions were based on monthly capture data. Sex ratios for subadults and adults were calculated separately but were not reported unless statistically different. Deviations from the expected 1:1 ratio were tested for significance using  $\chi^2$  analysis.

Estimations of survivorship and longevity were made by examination of the mean and maximum number of days between the first and final captures. All individuals captured more than once were included in these calculations.

Body mass of species was examined when sufficient data were available. To examine possible seasonal differences or patterns in the distribution of body mass, data were compiled for each month.

Movement patterns of each species were examined by calculating the mean and maximum distance traveled between successive capture sites. All individuals captured more than once were included in these calculations. Reproductive data were based on external examination of captured animals and were not sufficient to permit analyses of annual cycles.

Patterns of habitat utilization were examined in terms of a species' use of three-dimensional space and choice of microhabitat. Use of three-dimensional space was examined in arboreal and semi-arboreal species only. The following variables were measured: *trap location*, general characterization of arboreal support (e.g., horizontal branch, tree fork, etc.); *trap slope*, relative slope of arboreal trap support over 1 m preceding the trap entrance; *trap height*, height above ground of the trap entrance; *support diameter*, diameter of arboreal support (to the nearest 10 mm) at the entrance of the trap. A  $\chi^2$  analysis was used to test whether these variables affected trap selection. Microhabitat preferences

Table 2.—*Description and sampling method for 13 habitat variables at Capetinga.*

Variable	Sampling method
Canopy height	Relative height of canopy on a 0–3 scale
Density of trees	Sum of the distances between station stake and “A” tree, and between “A” tree and “B” tree
Number of trees	Number of trees within a 5 m radius of the station stake
Number of tree species	Number of tree species within a 5 m radius of the station stake
Density of ferns	Relative density of ferns within a 5 m radius of the station stake on a 0–4 scale
Density of bamboo	Relative density of individual clumps of bamboo (woody grasses) within a 5 m radius of the station stake on a 0–4 scale
Density of grass	Relative density of grass ground cover within a 5 m radius of the station stake on a 0–4 scale
Density of vines	Relative density of vines and lianas on a 0–4 scale
Vine size 1	Presence of vines with a maximum diameter of 0–3 cm
Vine size 2	Presence of vines with a maximum diameter of >3–6 cm
Vine size 3	Presence of vines with a maximum diameter of >6–9 cm
Vine size 4	Presence of vines with a maximum diameter of >9–12 cm
Vine size 5	Presence of vines with a maximum diameter of >12 cm

Table 3.—*Relative composition of each principal component of microhabitat analysis at Capetinga. The first 13 variables are defined in Table 2; the last 13 are the mean values of surrounding traps.*

Variables	Components				
	I	II	III	IV	V
Canopy height	0.247	-0.222	0.079	-0.333	0.287
Density of trees	0.094	-0.400	0.121	-0.239	0.531
Number of trees	0.715	-0.024	-0.116	0.032	-0.306
Number of tree species	0.732	-0.003	-0.138	-0.042	-0.268
Density of ferns	-0.360	0.593	-0.044	-0.077	-0.007
Density of bamboo	-0.264	-0.358	0.060	0.603	-0.153
Density of grass	-0.003	-0.106	-0.297	-0.094	0.637
Density of vines	-0.110	-0.443	0.255	-0.331	0.169
Vine size 1	0.241	-0.523	-0.022	-0.143	0.004
Vine size 2	-0.199	-0.352	0.424	-0.350	-0.068
Vine size 3	-0.249	-0.317	0.543	-0.105	0.173
Vine size 4	-0.118	-0.209	0.649	0.313	0.144
Vine size 5	-0.003	-0.106	-0.297	-0.094	0.637
Sur. canopy height	0.397	-0.266	-0.418	-0.089	0.295
Sur. density of trees	0.058	-0.123	-0.557	0.056	-0.034
Sur. density of species	0.761	-0.121	0.245	0.059	0.024
Sur. density of ferns	-0.139	0.548	0.055	-0.104	0.370
Sur. density of bamboo	-0.252	-0.444	-0.082	0.641	-0.119
Sur. density of grass	0.123	0.395	-0.203	0.042	0.098
Sur. density of vines	-0.391	-0.192	-0.141	-0.423	-0.479
Sur. vine size 1	0.205	-0.497	-0.178	-0.388	-0.322
Sur. vine size 2	-0.421	-0.249	-0.185	-0.535	-0.295
Sur. vine size 3	-0.437	-0.313	-0.422	-0.125	0.164
Sur. vine size 4	-0.065	-0.388	-0.512	0.301	0.198
Sur. vine size 5	-0.126	-0.402	-0.421	0.430	0.048
Percent of character variance explained	13.6	11.6	10.7	9.0	6.9

were examined by using a  $\chi^2$  analysis to compare observed trapping frequencies in each microhabitat against the expected (based on the percentage of available traps in each microhabitat type).

## RESULTS

### *Microhabitats*

The first five principal components of the initial set of 26 habitat variables explained 51.8% of the variation (Table 3). Generalized trends were identified by examining the habitat variables with significant loadings (greater than  $\pm 0.5$ ). Table 3 can be summarized by noting that high positive loadings on Component I reflect a high density and diversity of trees, while negative loadings mean more open forest. Component II positive loadings indicate dense fern patches and the absence of slender vines. Positive loadings on Component IV indicate dense stands of bamboo and few surrounding vines, while Component V positive loadings mean that dense clumps of grass were present, along with a high density of trees, both of these being surrounded by areas of lower vegetation density. On each component, negative loadings reflect the opposite traits of positive loadings. Relative loadings of each component reflect six distinctive microhabitats (fern thicket, dense forest, vine tangle forest, forest mosaic, bamboo edge, and forest edge; Fig. 1). Components with loadings greater than  $\pm 0.20$  were also considered as contributing factors in the overall make-up of a microhabitat.

A cluster analysis of 26 habitat variables was performed to further define the

relationship that these microhabitats have with each other. Results were projected onto a dendrogram that clustered similar trap stations together (Fig. 2). The analysis shows a distinct dichotomy between the Fern Thicket and Bamboo Edge and the remaining microhabitats. The primary division separates the Fern Thicket from the others. The secondary division separates three trap stations that are characterized as having dense tangles of lianas and vines. These stations were located within the Vine Tangle Forest (station E12) and the Forest Mosaic (stations C13 and I8). The tertiary division separated the Bamboo Edge microhabitat from the others. Some structure is evident within the remaining group, such as the presence of a subcluster of Forest Edge trapsites within the larger cluster. The three types of semideciduous gallery forest (Dense Forest, Forest Mosaic, and Vine Tangle Forest) were not divisible by cluster analysis, suggesting that these microhabitats are not as distinctive as the ecotonal microhabitats (Bamboo Edge, Forest Edge, and Fern Thicket).

The Fern Thicket microhabitat was a cleared area at the north end of the grid (Fig. 1; 12% of the total area), where bracken fern (*Pteridium aquilinum*) formed extremely dense thickets 2 to 4 m in height. Other plants included low grasses, small vines, and sparsely scattered emergent trees, many of which were dead. This area received direct sunlight and experienced extreme daily temperature fluctuations, especially in winter when the temperature ranged from 3°C at night to 34°C during the day. The ferns formed a closed canopy and provided good cover for both arboreal and terrestrial mammals.

The Bamboo Edge microhabitat (13% of the grid) was situated along much of the gallery forest margin, where there were dense stands of woody bamboo (*Ichnananthus bambusiflorus*) forming a canopy at 5 m. This species was present throughout the grid, but was sparse inside the gallery forest. Trees were widely dispersed. Dominant tree species included *Belangeria glabra* and *Callisthene major*.

The Forest Edge microhabitat comprised 10% of the grid and was important in understanding the distributional patterns of the resident mammals. The transition from forest to savanna was rather abrupt, with the average width being 7 m. Here the tall grass of the campo intermingled with the thinning trees. Trees were large and leaned toward the adjoining campo, forming a wall that joined the gallery forest canopy with the substrate of the campo. The dominant tree species were *Belangeria glabra*, *Callisthene major*, and *Qualea dichotoma*. The undergrowth shrubs and saplings were dense. Herbaceous vines and lianas were abundant and acted as an arboreal network for climbing mammals.

Three types of semideciduous gallery forest occurred over the rest of the grid. At the south end was Dense Forest, representing 21% of the grid. This was the least disturbed habitat and plant diversity was high. The forest floor was bare except for scattered small shrubs and small trees. The 15-m high canopy was relatively closed, with few emergent trees. Common tree species were *Amaioua guianensis* and *Protium* sp.

The Forest Mosaic, a mixture of forest and light gaps, comprised 27% of the grid. Light gaps were formed either by natural tree falls or selective cutting by humans. In light gaps, the canopy was completely open and the sun shone directly on the forest floor. Undergrowth was thick and, in older gaps, became an impenetrable thicket. In between light gaps, the canopy was relatively open and ranged from 7 to 10 m in height. Large trees emerged above the forest canopy. Dominant emergent species were *Callisthene major*, *Copaifera langsdorfii*, and *Piptocarpha macropoda*. *Tapirira guianensis* was a common canopy-level tree.

The third type of forest was the Vine Tangle Forest (16% of the grid), and was

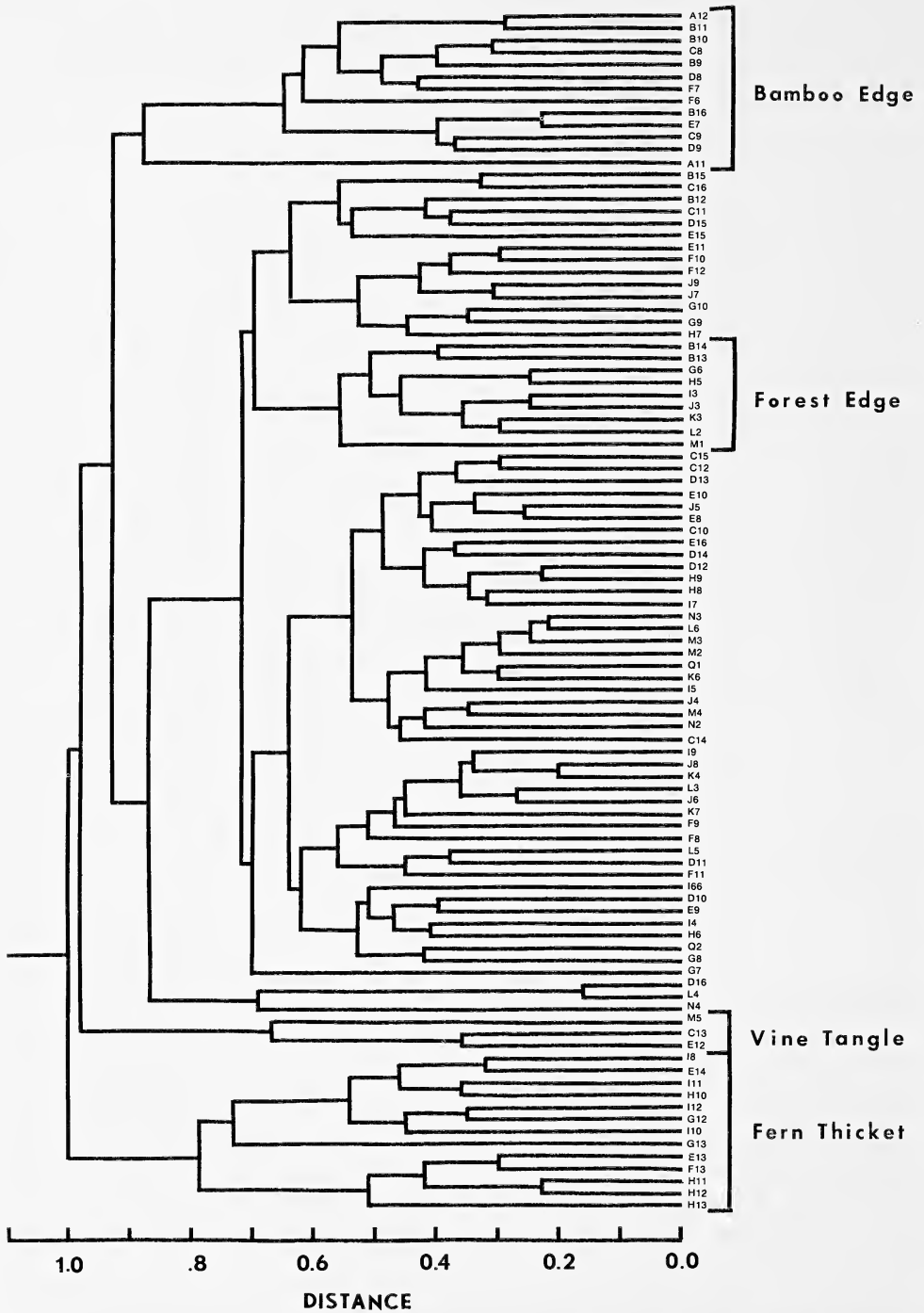


Fig. 2.—Distance dendrogram of 100 trap stations based on characters and clustered by unweighted pair-group method using arithmetic averages. The cophenetic correlation is 0.85.

characterized by large trees having dense tangles of vines and lianas to a height of 4 m. Common tree species were *Piptocarpha macropoda* and *Xylopia aromatica*. This microhabitat seemed to be a more mature form of the forest mosaic. Throughout the grid, neither palms nor epiphytes were common. *Salacia elliptica* was one of the most common subcanopy trees. Alongside the creek, *Piper* sp. and a grass (*Panicum* sp.) were common undergrowth plants.

### Species Accounts

During seven months of trapping, 118 individuals were caught 731 times, including two species of marsupials and eight species of rodents. *Marmosa agilis* and *Monodelphis americana* were the marsupials, and the rodents were *Oryzomys bicolor*, *Oryzomys capito*, *Oryzomys concolor*, *Oryzomys nigripes*, *Rhipidomys mastacalis*, *Akodon cursor*, *Bolomys lasiurus*, and *Oxymycterus roberti*.

*Marmosa agilis*.—This small nocturnal didelphid marsupial ranges widely in the Cerrado region. It is generally associated with mesic areas, such as gallery forests and orchards and was the most commonly caught species at the Capetinga study site. Although primarily arboreal, 18% of the captures were in terrestrial traps. Individuals always escaped upon release by way of trees and vines. *M. agilis* had the longest mean residency of any of the small mammal species on the grid and had the greatest mean number of captures per individual (Table 4). Average mass and biomass estimates are given in Tables 5 and 6. *M. agilis* is insectivorous and frugivorous (Nowak and Paradiso, 1983); this was supported by observations of a captive individual that accepted a wide variety of fruits and insects.

Fourteen males and only two females were caught over six months. One of the females was captured 37 times. Neither female seemed to reach adulthood during the study period; however, accurate aging of females was difficult since the vaginal opening is internal. Females lack a true pouch and teats remain hidden when not lactating. Neither of the two females was ever observed to lactate during the study period. During the first 4 months of the study, the only males caught were subadult, identified by their relatively small size and the hairy condition of their scrotums. From May onward, males began to show signs of sexual maturity; their growth rate began to stabilize, the testes enlarged significantly, and the scrotum lost its hairy appearance and turned a blue-gray color. In June and July, all unmarked males that appeared on the grid were fully mature adults.

*Marmosa agilis* was a resident species; 50% of the individuals were caught in three or more consecutive months. Their ranges tended to shift slightly each month and overlapped with other individuals at the margins. Adults traveled significantly further than subadults between successive captures (41.1 m vs. 28.9 m; Student's *t*-test,  $P < 0.01$ ).

*Marmosa agilis* was caught in all six microhabitats (Table 7). The  $\chi^2$  analysis showed that its distribution across the grid differed significantly from that predicted if habitats had been used randomly ( $P < 0.01$ ). However, when the fern thicket microhabitat was removed from the analysis, the distribution was random. Therefore, it seems that *M. agilis* was actively avoiding the fern thicket and not distinguishing among the other microhabitats. Considering that *M. agilis* was strongly arboreal, these findings are not surprising. The fern thicket was the only microhabitat analyzed that was located outside the forest. Arboreal access was limited in this area.

Analysis of three-dimensional space requirements showed that *M. agilis* entered

Table 4.—Mean number of captures, percent arboreal, length of residency (in days), and mean distance (in meters) traveled between consecutive captures for small mammals caught at Capetinga.

Species	Number of individuals	Mean no. captures	Percent arboreal	Residency		Distance	
				Mean	Maximum	Mean	Maximum
<i>Marmosa agilis</i> <sup>a</sup>	16 (192) <sup>b</sup>	12.0 ± 12.7 <sup>c</sup>	82	56.1 ± 59.4	160	41.1 ± 35.0	142.1
<i>Monodelphis americana</i>	9 (33)	3.7 ± 5.4	0	17.2 ± 37.3	110	28.9 ± 19.0	89.4
<i>Oryzomys bicolor</i>	8 (22)	2.8 ± 2.3	86	23.8 ± 47.9	140	35.8 ± 26.1	128.1
<i>O. capito</i>	14 (68)	4.9 ± 4.5	3	33.2 ± 39.8	143	45.2 ± 44.2	136.0
<i>O. concolor</i> <sup>d</sup>	8 (68)	8.5 ± 8.3	71	46.5 ± 39.3	94	18.4 ± 16.2	67.1
<i>O. nigripes</i>	23 (134)	5.8 ± 6.0	30	28.8 ± 35.3	116	45.3 ± 25.9	107.7
<i>Rhipidomys mastacalis</i>	3 (7)	2.3 ± 1.5	100	—	—	25.9 ± 15.4	53.9
<i>Akodon cursor</i>	10 (53)	5.2 ± 5.2	0	49.3 ± 60.1	147	27.3 ± 22.7	106.0
<i>Bolomys lasiurus</i> <sup>e</sup>	22 (141)	7.0 ± 6.5	2	31.0 ± 30.9	88	—	—
<i>Oxymycterus roberti</i>	5 (13)	2.6 ± 2.6	0	—	—	32.4 ± 37.2	142.1
						27.5 ± 40.2	162.0
						10.2 ± 9.5	31.6

<sup>a</sup> First distance for 54 adults; second for 122 subadults.  
<sup>b</sup> Number of individuals captured (total number of captures).  
<sup>c</sup> Mean ± one standard deviation.  
<sup>d</sup> First distance for 26 males; second for 16 females.  
<sup>e</sup> First distance for 51 males; second for 42 females.

Table 5.—Average mass (grams) for each species of small mammal at Capetinga.

Species	Average mass	
	Adult	Subadult
<i>Marmosa agilis</i>	26.4 ± 5.7 <sup>a</sup> 15.0–36.0 (26) <sup>b</sup>	16.2 ± 3.3 6.5–24.0 (45)
<i>Monodelphis americana</i>	19.5 (1)	14.1 ± 2.6 9.5–18.0 (12)
<i>Oryzomys bicolor</i>	28.4 ± 4.0 21.0–53.0 (11)	17.0 ± 5.3 10.0–22.0 (4)
<i>O. capito</i>	58.7 ± 7.7 42.0–72.0 (17)	33.5 ± 16.6 12.0–65 (4)
<i>O. concolor</i>	58.8 ± 7.1 41.0–72.0 (19)	42.6 ± 5.8 36.0–50.0 (9)
<i>O. nigripes</i>	22.6 ± 4.4 16.0–33.0 (39)	12.7 ± 3.0 6.0–18.0 (19)
<i>Rhipidomys mastacalis</i>	68.0 (1)	27.5 12.0–43.0 (2)
<i>Akodon cursor</i> <sup>c</sup>	47.2 ± 4.9 39.5–57.0 (15) 38.0 ± 1.6 36.0–40.0 (14)	21.5 ± 6.4 12.5–26.0 (4)
<i>Bolomys lasiurus</i>	42.2 ± 7.5 33.0–63.0 (33)	30.8 ± 3.4 21.0–35.0 (14)
<i>Oxymycterus roberti</i>	71.0 ± 3.8 66.0–75.0 (4)	55.0 52.0–58.0 (2)

<sup>a</sup> Mean ± one standard deviation.<sup>b</sup> Range, with sample size in parentheses.<sup>c</sup> First average mass for adult males; second for adult females.

traps set on fern fronds less frequently than expected ( $P < 0.01$ ). These results agree with the macrohabitat data. *M. agilis* had a preference for traps set on branches 20–40 mm in diameter ( $P < 0.01$ ) and entered traps randomly without regard to support angle or height.

Cotton balls were provided in all traps for insulation, but *M. agilis* never used the material to make temporary nests. During the cool winter mornings, this species often was found torpid in the traps. Torpidity was apparently an effective response against low temperatures; despite the lack of an insulating nest, *M. agilis* had the lowest rate of trap mortality.

*Monodelphis americana*.—This small terrestrial didelphid is widespread throughout eastern Brazil (Nowak and Paradiso, 1983), although little information is available on its ecology. Both sexes have three dark stripes on the dorsum, and females lack a true pouch.

At the Capetinga study site, *M. americana* was relatively uncommon. It was highly transient, with only two individuals (22%) caught more than twice. Individuals were found in traps during most of the late afternoon trap checks, suggesting that they are active during the day. Only one adult (a male) was trapped; all other individuals were subadults. The sex ratio of *M. americana* caught in traps on the grid was 8:1.

Animals were caught during all the months that terrestrial traps were set. The sample size was too small to test for significance of microhabitat preference. Nevertheless, this species did not seem to show strong preference for any particular

Table 6.—Monthly biomass estimates (g/ha) based on the minimum number of known individuals for 10 small mammal species from Capetinga. Mean of *Marmosa agilis* computed for months of January through July; means for all other species computed for February through July. Number of individuals/month given in parentheses.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Mean
<i>Monodelphis americana</i>	—	56 (4)	42 (3)	10 (1)	47 (3)	16 (1)	20 (1)	32
<i>Marmosa agilis</i>	67 (5)	79 (5)	92 (6)	123 (7)	122 (6)	142 (6)	258 (9)	126
<i>Oryzomys bicolor</i>	—	137 (5)	103 (5)	54 (2)	28 (1)	29 (1)	30 (1)	63
<i>O. capito</i>	—	358 (10)	319 (7)	185 (4)	55 (1)	63 (1)	192 (3)	195
<i>O. concolor</i>	—	64 (1)	94 (2)	161 (4)	150 (3)	276 (5)	309 (5)	176
<i>O. nigripes</i>	—	18 (1)	117 (6)	162 (9)	136 (7)	149 (10)	241 (11)	137
<i>Rhipidomys mastacalis</i>	—	110 (2)	—	—	—	68 (1)	—	30
<i>Akodon cursor</i>	—	127 (3)	84 (2)	191 (5)	117 (3)	205 (5)	242 (5)	161
<i>Bolomys lasiurus</i>	—	—	—	198 (4)	290 (7)	467 (12)	558 (16)	252
<i>Oxymycterus roberti</i>	—	75 (1)	72 (1)	58 (1)	—	—	125 (2)	55
Total	67	969	923	1142	945	1415	1975	

microhabitat. *M. americana* did not have a torpidity response to low temperatures, not did it make use of the cotton provided in each trap. Trap mortality was high on cool nights.

*Oryzomys bicolor*.—This nocturnal cricetid rodent ranges from Panama to tropical South America east of the Andes (Handley, 1976; Honacki et al., 1982; Patton et al., 1982). Within this range, it inhabits unflooded evergreen forest (Alho, 1982) and is sometimes found in native dwellings (Husson, 1978). It has fleshy thick-padded feet characteristic of arboreal rodents. During this study it was captured in ground traps only three times (14% of captures).

Eight individuals (6 males and 2 females) were captured 22 times. Three of the eight (37%) were caught in more than one trapping period and only one was captured for more than two periods. In other areas, this species has also been difficult to recapture. For example, in Venezuela, 71% were never recaptured (O'Connell, 1979). Of all the species present on the grid, *O. bicolor* traveled the greatest mean distance between successive captures (Table 4). The sample size was not large enough to test for microhabitat preferences. No preference was shown for specific traps based on their height or slope ( $\chi^2$  test,  $P > 0.05$ ).

*Oryzomys capito*.—This species is common throughout the Neotropics and can be found in nearly all habitats, including campo, cerrado, dry and humid forests, agricultural fields, as well as in houses (Alho, 1981; Handley, 1976; Mares et al., 1981a; Mello and Moojen, 1979; Moojen, 1966). During the seven months of trapping, six females and eight males were caught a total of 68 times. Only three percent of the captures were made in arboreal traps. Forty-four percent of the



Table 7.—Percent of captures made in each of the following microhabitats: BE, Bamboo Edge; DF, Dense Forest; FE, Forest Edge; FM, Forest Mosaic; FT, Fern Thicket; VT, Vine Tangle Forest.  $n$  = number of captures.  $\chi^2$  test; \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , nt = not tested.

Species	n	Microhabitats						$\chi^2$
		BE	DF	FE	FM	FT	VT	
<i>Monodelphis americana</i>	34	15	23	15	23	6	18	nt
<i>Marmosa agilis</i>	192	20	21	10	27	4	18	**
<i>Oryzomys bicolor</i>	22	0	14	5	45	0	36	nt
<i>O. capito</i>	68	6	38	7	43	0	6	**
<i>O. concolor</i>	68	1	6	3	15	59	16	*
<i>O. nigripes</i>	133	14	30	11	12	26	7	**
<i>Akodon cursor</i>	52	2	52	17	8	13	8	**
<i>Bolomys lasiurus</i>	141	42	6	46	6	0	0	**
Percent expected		13	21	10	27	12	17	

marked animals were caught in only one trapping period. In February and March (late wet season), it was the most commonly caught species on the grid; in May and June (mid-dry season), it was one of the rarest.

*Oryzomys capito* was caught in all areas of the grid, except the fern thicket. The  $\chi^2$  analysis indicated that this species was trapped in dense forest and forest mosaic more frequently (81% of all the captures) than would be expected by chance (Table 7).

*Oryzomys concolor*.—This species is found in tropical forests and marsh-forest complexes from southern Costa Rica to northern Argentina (Alho, 1982; Honacki et al., 1982; Paula, 1983; Pine, 1973). At the Capetinga study site, it was the largest arboreal rodent species caught on the grid.

Six males and two females were captured 68 times. Although *O. concolor* has the well-padded feet characteristic of arboreal rodents, 29% of the captures were in ground traps. All captures were made at night. Six individuals (75%) were caught in two or more trapping periods. *O. concolor* had the longest mean length of residency of all the small rodents on the grid (Table 4). There was a significant sex and age difference in the mean distance traveled between consecutive captures. Mean distance for adult males was 45.3 m, whereas for adult females, it was only 25.9 m (Student's  $t$ -test,  $P < 0.01$ ). Adults of both sexes traveled a mean distance of 37.2 m; subadults traveled 22.9 m (Student's  $t$ -test,  $P < 0.05$ ).

*Oryzomys concolor* was quite specific in its habitat preference. Seventy-five percent of all captures were made either in the fern thicket or in traps adjacent to this microhabitat. It was caught more frequently in traps set on fern fronds than was expected by chance ( $P < 0.01$ ). It showed a similar preference for traps that were set on supports less than 10 mm in diameter ( $P < 0.01$ ); fern petioles never exceeded 10 mm in diameter. Home ranges overlapped only slightly in the cleared patches of forest.

Analysis of the three-dimensional space usage showed that *O. concolor* entered traps set at less than 45° more frequently than expected. Trap height was not important.

*Oryzomys nigripes*.—This small cricetid rodent commonly inhabits cerrado, dense brush, gallery forests, coastal scrub, pastures, agricultural fields, and human dwellings (Alho, 1981, 1982; Mares et al., 1981a, 1981b; Mello, 1969, 1977; Mello and Moojen, 1979; Veiga-Borgeaud, 1982). At Capetinga, it was the smallest

rodent on the grid and one of the most commonly trapped species. During the course of this study, 23 individuals (8 females and 15 males) were captured 134 times. *O. nigripes* had one of the shortest mean residencies (28.8 days; Table 4). Over half (52%) of the marked individuals were caught in only one trapping period; 26% were caught only once.

*Oryzomys nigripes* exhibited a significant preference for the fern thicket and the dense forest ( $P < 0.01$ ). It entered traps in the forest mosaic less often than expected. Analysis of traps set at specific heights revealed that *O. nigripes* preferred traps set within 1 m of the ground. This species was primarily terrestrial. The slope of the trap was not important.

*Rhipidomys mastacalis*.—This species is found primarily in mesic forests (Alho, 1981, 1982; Dietz, 1983; Fonseca and Redford, 1984; Handley, 1976; Mello, 1969; Mello and Moojen, 1979). During this study, all captures were made in arboreal traps.

Only three individuals (two males and one female) were captured a total of seven times, making *R. mastacalis* the least frequently captured small mammal. None was caught in more than one period and all captures were made at night. This species was captured only in the months of February and June, corresponding to early and mid-dry season.

*Akodon cursor*.—This cricetid rodent is a heavy-bodied, vole-like mouse that is found throughout the Cerrado region in gallery forests and cultivated fields (Mello, 1969; Moojen, 1952). It is completely terrestrial. Three females and seven males were caught a total of 53 times. In spite of the long mean residency (Table 4), 50% of the individuals were never caught a second time and thus were not included in the calculation of residency length. Only one individual was caught in more than two trapping periods.

Adult males weighed significantly more than females (47.2 vs. 38.0 g; Student's *t*-test,  $P < 0.05$ ). There was no significant difference in the mass of subadult males and females. At Capetinga, subadults were captured only from April through June, suggesting that young are born in the late wet season (ca. February and March). Fifty-two percent of the captures of *A. cursor* were made in dense forest; this was statistically higher usage than would be predicted if the animal randomly frequented microhabitats (Table 7).

*Bolomys lasiurus* (= *Zygodontomys lasiurus*).—This cricetid rodent is common in nearly all habitats, both disturbed and natural (Alho, 1981; Dietz, 1983; Mares et al., 1981a; Mello and Moojen, 1979; Moojen, 1966). At the Capetinga study site, it was very common; 22 individuals (13 females and 7 males) were caught 141 times. Every month, 50% of the active individuals were previously unmarked, suggesting that turnover was high. Only two individuals were not recaptured at least once.

*Bolomys lasiurus* is almost exclusively terrestrial. One individual was trapped twice in the same arboreal trap; this trap was set on a fallen tree less than 1 m above the ground. Even though there are several previous studies concerning this species (e.g., Alho, 1979, 1981; Alho and Souza, 1982; Almeida et al., 1981; Pereira, 1982; Souza, 1979; Souza and Alho, 1980), there are no other reports of *B. lasiurus* being captured in arboreal traps.

*Bolomys lasiurus* had the lowest mean distance traveled of any species in the study. This was due, in part, to *B. lasiurus*' tendency to enter certain traps more than others; four adjacent traps located within 1 m of the tall dense grass of the

cerrado accounted for 39% of the captures. Adult males traveled significantly further than adult females (Table 4).

On 12 occasions, the traps were checked twice each day; once early in the morning and again in the late afternoon. Every afternoon check revealed one to three *B. lasiurus*; generally, these were animals not found in traps during that day's morning check, suggesting that most individuals were diurnal. In a related study, Lacher et al. (in press) found this species to be diurnal in cerrado grassland habitat.

*Bolomys lasiurus* was absent from the grid during the first three trapping periods (January–March 1984) and was first trapped in April. Thereafter, the number of individuals increased dramatically, until by June it was the most commonly encountered species. Adults began to appear in April and new adults continued to be marked in the ensuing months; subadults were not captured before May. The sex ratio of captured *B. lasiurus* was 4.1:1.

At Capetinga, *B. lasiurus* was quite specific in its microhabitat preferences; distribution across the grid varied significantly from the expected (Table 7). Eighty-eight percent of all captures were made in two microhabitats: the forest edge and the bamboo. These two areas were located on the edge of the grid that bordered the savanna. It was never trapped beyond the forest edge, entering the gallery forest only at certain points and never very far.

*Oxymycterus roberti*.—This species is a characteristic resident of brejos, the permanently inundated savanna that borders gallery forest. Several authors state that typically it is confined to this habitat and is only rarely caught in adjacent areas (Borchert and Hansen, 1983; Fonseca and Redford, 1984; Mathews, 1977; Redford, 1984), although T. E. Lacher (personal communication) caught it frequently in campo limpo. At the Capetinga study site, there was no bordering brejo, yet *O. roberti* was trapped on the grid.

Five individuals were caught a total of 13 times; all were males. None of the marked animals seemed to be resident in the study area. Three were caught only once and none was caught in more than one trapping period. All but one capture was made in the part of the grid that was dominated by bracken fern; one individual was caught inside the gallery forest. Individuals were caught in four of the seven months; the species was uncommon in both the dry and wet seasons.

## DISCUSSION

### *Small Mammal Diversity*

Previous workers have noted that the gallery forest is the most complex habitat in the Cerrado region (Fonseca and Redford, 1984; Mares et al., 1986; Ratter, 1980). In this study, eight species of rodents and two species of marsupials were caught in gallery forest habitat. In an earlier live-trapping study at the Fazenda Água Limpa, Alho (1981) surveyed the rodents of three other habitats. In the cerrado (s.s.), three species of rodents were trapped; in the campo, there were four, and in the cerradão, there were also four. In a related study in a different gallery forest, Mares et al. (1986) found seven rodent species in the gallery forest and six in the campo. Thus, gallery forest is generally richer in species than the other kinds of Cerrado habitats. Of the rodent species Alho (1981) caught, only *Calomys callosus* was not caught during this study. *O. nigripes* (= *O. elurus*) was captured both inside and outside the gallery forest in sizeable numbers; it was considered

to be a habitat generalist (Alho, 1982). *B. lasiurus* was caught in all four habitats, but is not considered a regular inhabitant of the gallery forest.

### *Didelphid Life History*

Earlier studies have noted that the life expectancy of some *Marmosa* species is approximately 1 year (Hunsaker, 1977; Nowak and Paradiso, 1983). Further evidence suggests that only one litter is produced in a lifetime (Enders, 1935). The data presented here imply that *M. agilis* may breed only once annually. During the entire study, all males gained weight at the same rate and passed through various stages of development at the same time (Fig. 3). In the early half of the study, all males were judged to be subadults. They began to show indications of maturity in May, and by June and July, all males caught on the grid were fully mature adults. During the latter months of the study, the only animal remaining on the grid was a lone female we judged to be a subadult (based on body size). She weighed 14.0 g on her first day of capture (23 February), reached a mass of 19.0 g by late April, and did not gain weight thereafter. She was captured periodically until the study ended. *M. americana* exhibited a similar growth pattern. During most of the study, only subadults were captured. A single adult male was captured once in July.

Data for *M. agilis* and *M. americana* indicated sex ratios that were strongly skewed (7:1 and 8:1, respectively). Although this difference was statistically significant, it may have been an artifact of the differential activity of each sex. Males might be more active, inquisitive, or aggressive, and females might not be as rare as the trapping record suggests. In Venezuela, adult male *M. cinerea* were trapped six times as frequently as adult females, and lactating females were never captured (O'Connell, 1979; August, 1981). A lactating female's movement may be hampered by the physical burden of young, and her foraging radius may be reduced. At Capetinga, the only females of either species caught were subadults, suggesting that *M. agilis* and *M. americana* were behaving in a similar manner.

*Marmosa agilis* was a long-term resident at Capetinga. This contrasted with what is generalized about didelphids, that they are "nomadic, solitary animals that do not consistently restrict their activities to any particularly areas" (Hunsaker, 1977:119). During this study, most *M. agilis* individuals remained on the grid for three or more months. Their ranges shifted slightly every month and a few individuals seemed to eventually shift enough to be off the grid. *M. agilis* did not seem to have mutually exclusive territories, since ranges overlapped with each other.

### *Demographic Patterns*

Demographic patterns varied from species to species. *R. mastacalis* seemed to be present on the grid on a seasonal basis. At Capetinga it was only caught in February and June, whereas at Parque Nacional de Brasília, it was caught in May, June, and July (dry season; Paula, 1983). Dietz (1983) noted that 90% of the captures of *R. mastacalis* at Parque Nacional Serra da Canastra, Minas Gerais, Brazil, were made in the dry season. If it did not migrate up into the canopy or to other gallery forest sites during the months when it was absent from the gallery forest study area, it probably moved to a habitat having a pronounced arboreal component, such as cerradão.

*Oxymycteris roberti* was caught at Capetinga within the fern thicket microhabitat during the wet season, and twice in the forest mosaic during the dry season.

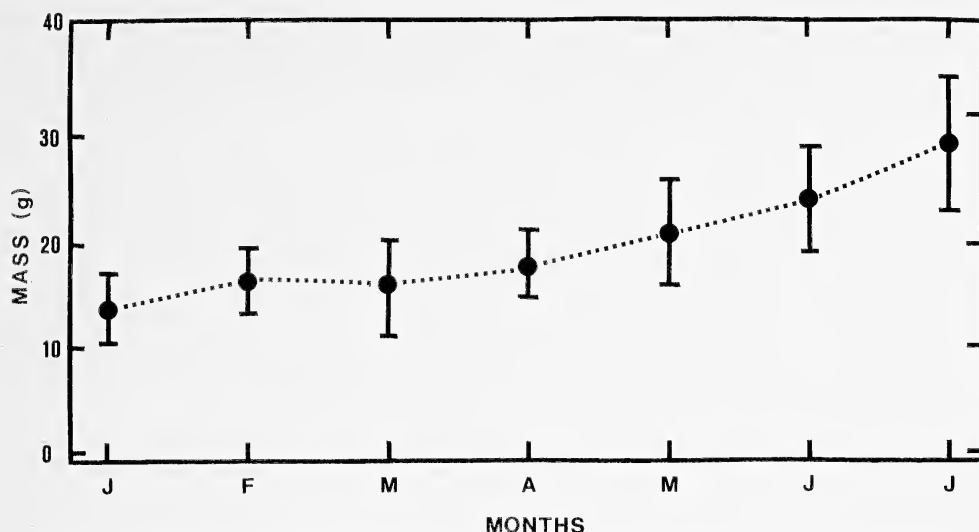


Fig. 3.—Mean monthly weight (grams  $\pm$  SE) of *Marmosa agilis* males over course of study.

Alho (1981) caught it a few times in the gallery forest; Borchert and Hansen (1983) and Paula (1983) noted that it was trapped in low numbers in all habitats except gallery forest.

Paula (1983) reported on seasonal movements of small mammals in gallery forest and campo habitats at Parque Nacional de Brasília, approximately 25 km from the Capetinga study site. He trapped from February to September, roughly the same time period as the Capetinga study. Six species of small mammals (defined as  $<120$  g mean mass) were caught at his study site; these same six were also caught at Capetinga. *O. bicolor*, *A. cursor*, and *O. roberti* were not captured in the gallery forest at Parque Nacional de Brasília. *M. agilis* was extremely common, even though Paula only sampled with terrestrial traps. In the wet season, this species was caught primarily in the dry gallery forest; whereas, in the dry season, it moved to the wet gallery forest. At Capetinga, seasonal movements were not evident for *M. agilis*; it remained common in the gallery forest during all the months of the study.

*Bolomys lasiurus* was captured only from April onward (fourth month of trapping). Even so, its biomass increased rapidly until by July it was 558 g/ha (Table 6); by then, it became the dominant small mammal species on the grid. Since the forest margin, its preferred habitat, represented only 0.25 ha of the grid, its biomass per ha of preferred habitat during that month was 2232 g/ha, or approximately 50 individuals per ha of forest margin. This is impressive when one considers that the number of individuals/ha increased from 0 to 50 in just 4 months. Other studies have noted that populations of *B. lasiurus* fluctuated. Mello (1980) found that this species was absent from her grid during the spring of one year and abundant the following spring. In Exu, state of Pernambuco, populations were monitored periodically through several years. From 1967 to 1971, the density of *B. lasiurus* reached 187 individuals  $\text{ha}^{-1}$   $\text{month}^{-1}$  (Karimi et al., 1976). Years later, in 1977, three months of trapping in the same general area (29,250 trap-nights) yielded only one individual (Streilein, 1982). Dietz (1983) reported that

populations were very low in the wet season in southern Minas Gerais state. At Capetinga, it seemed as if the population bloomed during the study period, forcing animals to migrate to suboptimal habitat, such as the ecotonal zone between the gallery forest and the grassland campo.

### *Distributional Patterns*

Six microhabitats were distinguished based on phytophysiognomic characters and, subsequently, on small mammal distribution patterns. Broadly speaking, these can be placed into three main groups: the fern thicket, the forest-savanna ecotone, and the gallery forest itself. The fern thicket was the primary habitat for *O. concolor* and was extensively used by *O. nigripes*. *O. roberti* was captured only on rare occasions, but nearly always in the fern thicket. Because *O. concolor* seemed to prefer disturbed habitat over the more pristine, one would expect their numbers to increase through small-scale forest destruction.

The forest-savanna ecotone was divisible into two microhabitats: the forest edge and the bamboo edge. Both were characterized as narrow strips of vegetation that contained elements common to both the forest and the savanna. None of the small mammal species differentiated between the two microhabitats, even though they were quite different phytophysiognomically. Both constituted the dominant microhabitats for *B. lasiurus*. Other studies conducted at the Fazenda Água Limpa suggest that the cerrado (s.s.) is the primary habitat for *B. lasiurus* (Alho, 1981; Souza, 1979), but it is caught in nearly all major habitats throughout its range (Alho, 1982). The other small mammal species did not show preferences for the ecotonal zone. *O. concolor* was caught in this area less than expected, but this was probably due to the relatively long distance that lay between the forest margin and the primary habitat for this species, the fern thicket.

The gallery forest proper was subdivided into three kinds of forest: dense forest, vine tangle forest, and the forest mosaic. Some small mammals appeared to distinguish the apparently subtle differences that marked these microhabitats. *A. cursor* had a clear preference for the dense forest, the least disturbed part of the grid. All 10 species were trapped in the forest mosaic and yet no one species showed a specific preference for it. The forest mosaic microhabitat was the least definable by statistical classification methods.

### *Interspecific Avoidance Mechanisms*

Several of the mammal species are very similar in appearance and are closely related taxonomically, creating a potential for resource competition. *A. cursor* and *B. lasiurus* are two such species. Physically they are quite similar, but the microhabitat preferences showed that the two species overlapped little. *A. cursor* preferred the inner forest, whereas *B. lasiurus* was a savanna species that entered the Capetinga gallery forest only at the forest-savanna ecotone. In addition, *B. lasiurus* seemed to be primarily diurnal, while *A. cursor* was nocturnal. Therefore, both spatial and temporal mechanisms minimize competition for resources.

Four species of *Oryzomys* coexisted on the study area. Several differences served to minimize resource competition between them. An obvious division was size: *O. bicolor* and *O. nigripes* are smaller-bodied (28.4 and 22.6 g, respectively), whereas *O. capito* and *O. concolor* are more than twice as large (58.7 and 58.6 g, respectively). Small and large rodents could select food items of different sizes and, thus, minimal niche overlap would occur. Within weight classes, spatial separation reduces the degree of interaction between species. *O. bicolor* was pri-

marily arboreal (86% of captures in trees); *O. nigripes* was primarily terrestrial (70% of captures on ground), thus allowing spatial separation. *O. capito* and *O. concolor* segregate in a similar manner: *O. capito* was almost exclusively terrestrial (97% of captures on the ground), whereas *O. concolor* was arboreal (71% of captures in the trees). In addition, they showed different habitat preferences. *O. concolor* strongly preferred the fern thicket, whereas *O. capito* was never caught there. *O. capito* exhibited a preference for the dense forest and forest mosaic, while *O. concolor* ventured into these areas only occasionally. Thus, although both species were present in high numbers and lived in close proximity, interaction was probably a rare occurrence.

Our research is not definitive, but it allows us to begin to understand the ecology of the small mammal fauna of a little-studied habitat, the gallery forest of the Brazilian Cerrado. Although the gallery forest appears rather homogeneous at first glance, there are distinct microhabitats within the forest and the small mammals have responded to these by preferring one over another. This microhabitat preference and the fact that several species are ground dwellers, others are arboreal and some occur both in the trees and on the ground, help account for the fairly rich species composition of mammals in this narrow habitat, that extends only from 100 m to 1 km in width. Our preliminary findings suggest that habitat selection by small mammals is quite important in the tropical gallery forest at permitting coexistence, perhaps by reducing competition. Additional research should allow us to formulate a more detailed understanding of coexistence and species richness in this extensive and important tropical habitat.

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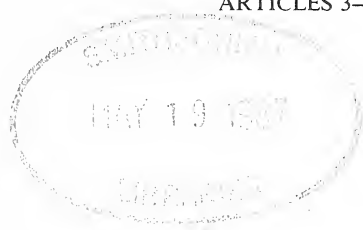
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## CONTENTS

- Art. 3. Reproduction in a Spanish population of *Acanthodactylus erythrurus* (Reptilia: Lacertilia: Lacertidae) ..... **Stephen D. Busack and Lorrie L. Klosterman** 97
- Art. 4. Karyotypic analysis of five rodents and a marsupial from Belize, Central America ..... **David W. Burton, John H. Bickham, Hugh H. Genoways and Timothy J. McCarthy** 103
- Art. 5. Biosystematic studies in *Stenanthium* (Liliaceae: Veratreae). I. Floral morphology, floral vascular anatomy, geography and taxonomy of *S. occidentale* A. Gray ..... **Frederick H. Utech** 113
- Art. 6. Results of The Carnegie Museum of Natural History Expeditions to Belize. III. Distributional notes on the birds of Belize ..... **D. Scott Wood and Robert C. Leberman** 137
- Art. 7. A review of the crane flies in the Subgenus *Tipula* (*Papuatipula*) (Diptera: Tipulidae), with descriptions of five new species ..... **Chen W. Young** 161

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**THE CARNEGIE**  
MUSEUM OF  
NATURAL HISTORY

REPRODUCTION IN A SPANISH POPULATION OF  
*ACANTHODACTYLUS ERYTHRURUS*  
(REPTILIA: LACERTILIA: LACERTIDAE)STEPHEN D. BUSACK<sup>1,2</sup>

Research Associate, Section of Amphibians and Reptiles

LORRIE L. KLOSTERMAN<sup>3</sup>

## ABSTRACT

Reproduction in male *Acanthodactylus erythrurus* from La Algaida, Cádiz Province, Spain, is characterized by spring spermiogenesis, copulation between June and August, and post-mating spermatogenesis that begins shortly after the testes are evacuated and continues through the fall. Vitellogenic growth of ovarian follicles begins in the spring, prior to mating. Vitellogenesis proceeds for a period of about one to two months, oviductal eggs are first seen in early June, and hatchlings first appear during August. Clutch size ranges between one and five ( $\bar{x} = 3$ ) and larger females tend to produce larger clutches. No direct evidence for multiple clutches was found.

## INTRODUCTION

Several aspects of the ecology of *Acanthodactylus erythrurus* at La Algaida, Spain, have been described (Busack, 1976; Pough and Busack, 1978; Busack and Jaksić, 1982), but no reproductive data have been published. We undertook this study of reproduction in the population to fill this gap in our knowledge of its life-history, and to compare reproductive parameters with those of the Moroccan population of this species (Bons, 1962, 1963, 1964, 1967, 1969, 1972).

## MATERIALS AND METHODS

Specimens were collected from La Algaida (25.5 km [AIR] NW Jerez de la Frontera, Cádiz Province, Spain) between May 1970 and November 1971 (see Busack and Jaksić, 1982, for details). Each individual was preserved immediately in 10% formalin and later transferred to 70% ethyl alcohol for permanent storage. Busack and Jaksić (1982) determined that all males  $\geq 61$  mm snout-vent length (SVL), and all females  $\geq 57$  mm SVL, in this population were adult; only males and females of these SVLs or larger were used to assess seasonal reproductive changes.

Testes from individuals collected from March through October were prepared following procedures described by Berg (1953), sectioned, and examined microscopically for the cellular stages of spermatogenesis. Length of the left testis was measured *in situ* with an ocular micrometer, and testis volume in 140 adult males was determined by fluid displacement. Seminiferous tubule diameter was measured in 15 adult males collected from March–October, and the diameters of up to 30 tubule cross-sections were used to calculate average tubule diameter. We did not examine efferent ducts or epididymides for the presence of spermatozoa. In this species spermatozoa appear to pass rapidly through these structures (Bons, 1969), thus testis condition serves as a reliable indicator of the timing of mating.

Ovarian follicles were measured *in situ* with an ocular micrometer in 95 adult females. Larger, slightly elongated, follicles were measured along the axis of elongation, and follicles in which the

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Submitted 1 August 1985.

diameter was  $\geq 0.5$  mm were recorded. The lengths of oviductal eggs were measured *in situ* with dial calipers accurate to 0.1 mm.

Estimates of clutch size are usually obtained by counting growing or preovulatory follicles present in ovaries during the breeding season (Fitch, 1970). Degeneration of large follicles has been observed in *A. erythrurus* (Bons, 1964) but atretic follicles were not conspicuous in females containing large yolky eggs examined during this study. By assuming that all vitellogenic follicles with a diameter  $\geq 3$  mm would be ovulated in a single clutch, we obtained an estimate of clutch size. Numbers of oviductal eggs and corpora lutea provided additional clutch size data.

Spearman rank correlation procedures were used to assess the relationship between lizard SVL and the number of developing follicles, corpora lutea, and oviductal eggs present. Resulting values of  $r_s$  were transformed according to Fisher's  $z$  transformation procedures and the probabilities presented are those for committing a Type I error in a two-tailed test.

*Specimens examined.*—The Carnegie Museum of Natural History (CM) 53245, 53282–53288, 53330, 53333, 53350, 53373, 53383, 53397, 53425, 53438, 53471, 53885–53886, 53888–53890, 53916, 54218–54220, 54223, 54225, 54256–54257, 54277, 54279, 54561, 54565, 54592, 54594, 54676, 54789, 54794, 54873, 55305–55328, 55337–55341, 55474, 55659, and 55699–55701.

## RESULTS

### *Male Reproductive Cycle*

Changes in both testis size and spermatogenic activity indicate a reproductive period from April to July. Testis length and volume reach a maximum between April and June and dramatically decrease during July. A gradual increase in size begins again in August and September and continues through October. By October, mean testis size had not yet reached that seen in the earliest spring collections (March), so we infer that additional testis growth took place during the winter when adults were inactive (Busack, 1976). Fig. 1 illustrates changes in testicular length and volume over the collecting period.

Histological examination confirmed that annual fluctuation in testis size and changes in diameter of seminiferous tubules are correlated with spermatogenic activity (Fig. 2). Maximal development of germinal epithelium and maximum tubule diameter occur from May through June. Seminiferous tubules contain several layers of primary spermatocytes in various stages of prophase, as well as numerous spermatids and spermatozoa (Fig. 2B), and spermatozoa are found only in tubule luminae during these months. Marked reductions in the height of the germinal epithelium and tubule diameter coincide with decrease in testis size in July, and seminiferous tubules often contain cellular debris (possibly the result of recent evacuation of spermatozoa) within the lumen. In most specimens the epithelium consists predominantly of a basal layer of spermatogonia and Sertoli cells (Fig. 2C). In a few specimens in which the tubule lumina contained cellular debris during June, primary spermatocytes were also abundant.

Proliferation of spermatogonia and development of primary spermatocytes occurs again during August. Although some August specimens contain only spermatogonia and Sertoli cells, others undergo active spermatogenesis (Fig. 2D). During the remaining months of the year, numbers of spermatogonia and spermatocytes present in seminiferous tubules increase. Large primary spermatocytes typically are distributed in basal clumps during September. Although some spermatocytes reach metaphase and telophase at this time, most spermatocytes are in earlier (leptotene and pachytene) stages of prophase during October. Although spermatogenesis resumes in some individuals as early as August, there are neither spermatozoa nor spermatids evident throughout the remainder of the year. The earliest appearance of spermatids is in April, just preceding the breeding season (Fig. 2A).



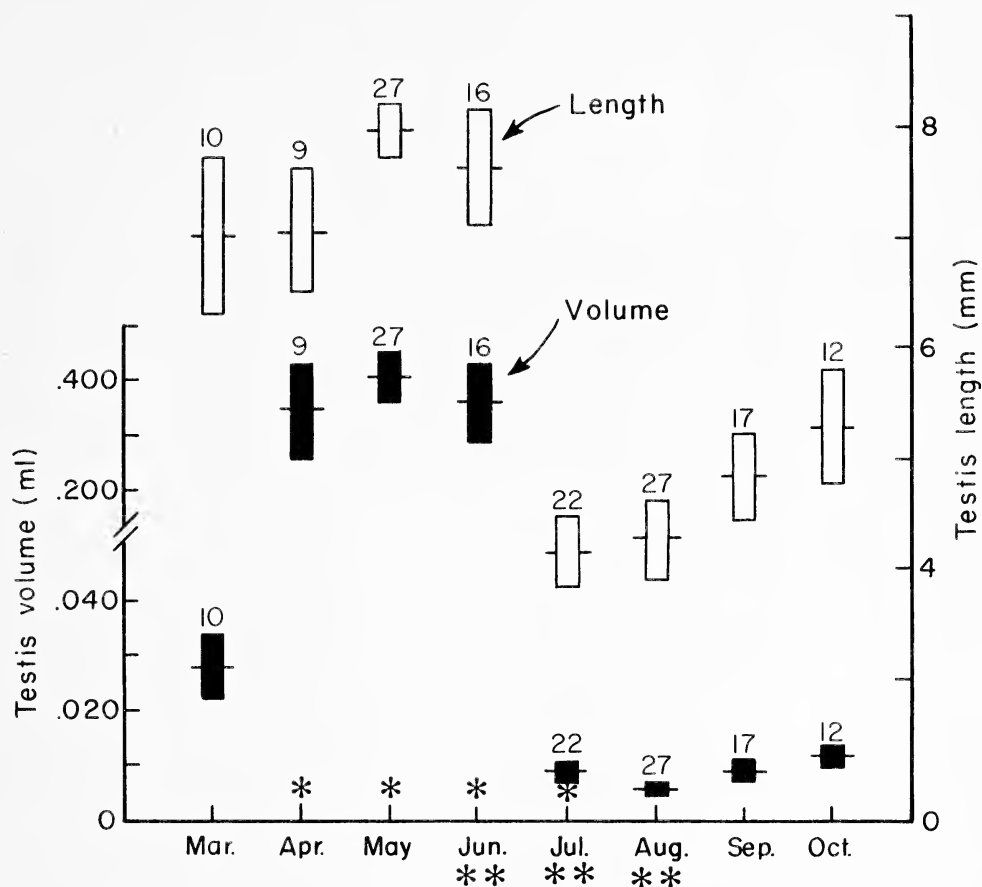


Fig. 1.—Seasonal changes in testis length and volume in adult male lizards. There were no statistically significant differences (Student's two-sample t-test) in testis length or volume between years, so monthly samples from both years are combined. Horizontal lines indicate monthly means,  $\pm$  two standard errors are indicated by the vertical bars, and sample sizes are indicated above the bars (\* = months in which some individuals contained testicular spermatozoa, \*\* = months in which individuals showed evidence for the recent evacuation of spermatozoa).

### *Female Reproductive Cycle*

Changes in maximum follicle size (Table 1) indicate a distinct seasonality in reproductive condition. Follicles measuring at least 2 mm in diameter are found during all months of the year in both ovaries of all adult females, and in months 2 mm is the maximum size of any follicle (Table 1). Follicles larger than this are vitellogenic, and are found in 20 of 22 females collected between late April and early July. One to three vitellogenic follicles are distinct (2.4–4.5 mm) in each ovary by mid-May. By late May and June follicles markedly larger than all others are presumably destined for ovulation. The maximum diameter attained by a vitellogenic ovarian follicle is 9.5 mm, undoubtedly near size at ovulation. Vitellogenic follicles are absent in ovaries containing corpora lutea.

Because vitellogenic ovarian follicles appear in some individuals as early as 18 April, we infer that the period of vitellogenesis is about two months in duration.

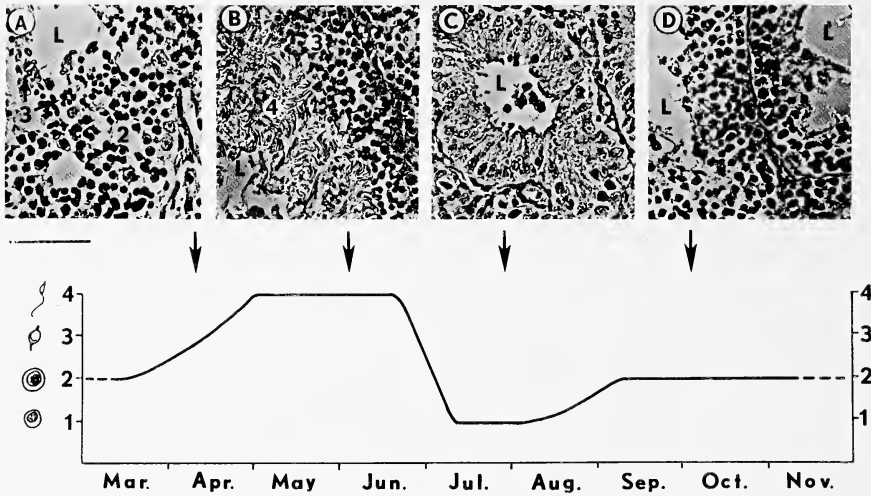


Fig. 2.—Seasonal changes in the seminiferous tubules of adult male *A. erythrurus*. Lower diagram illustrates the most differentiated stage of spermatogenesis in at least 50% of the individuals sampled. Numbered stages indicate the presence of: 1, spermatogonia and Sertoli cells only; 2, spermatogonia and primary spermatocytes; 3, developing spermatids in addition to the preceding cellular stages; 4, mature or nearly mature spermatozoa. Photomicrographs illustrate the appearance of the germinal epithelium in representative individuals collected on the dates indicated by the arrows. Scale bar below panel A = 0.05 mm; L identifies tubule lumen.

Oviductal eggs were first seen on 19 June. Shelled oviductal eggs measuring between 11.5 and 14.8 mm were found on 19 July, and the first hatchling lizards (SVL  $\leq 31$  mm) were found between 13 and 30 August during both years.

We found preovulatory follicles in 22 individuals, oviductal eggs in 6, and corpora lutea in 7 individuals. Estimates of mean clutch size derived from these data are 2.7 (range 1–5), 3.0 (2–4), and 2.7 (1–4), respectively. Females in Spain lay from one to a maximum of five eggs per clutch and the average clutch is about 3 eggs.

The relationship between SVL and number of vitellogenic follicles demonstrates probable differences in reproductive potential for lizards of different sizes. When all follicles with a minimum diameter of  $\geq 3$  mm are considered presumptive eggs, a significant relationship between SVL and clutch size is identified ( $z = 1.12$ ,  $N = 22$ ,  $P \ll 0.05$ ). The number of corpora lutea, which probably provides a more accurate estimate of clutch size, also shows a statistically significant correlation with SVL ( $z = 2.03$ ,  $N = 7$ ,  $P \ll 0.05$ ). No significant correlation between SVL and the number of oviductal eggs, however, was identified ( $z = 0.64$ ,  $N = 6$ ,  $P > 0.2$ ).

#### DISCUSSION

Reproduction in *A. erythrurus* at La Algaída occurs in late spring and summer. Although we did not observe mating in the field, the reproductive condition of both males and females indicates breeding capability between late May and early July. Seasonal changes in testis size (length and volume) and spermatogenic activity indicate a single copulatory period for males annually. Males begin reproductive activity (spermatozoa present in seminiferous tubules) during April, and

Table 1.—Monthly summary of follicle development and the distribution of oviductal eggs and corpora lutea among adult female *A. erythrurus* at La Algaída, Spain.

Month	Number of adult females in which maximum developing follicle diameter (mm) was:					Number of oviductal eggs per individual			Number of corpora lutea per individual			
	1	2	3	4	≥5	2	3	4	1	2	3	4
Mar	—	4	—	—	—	—	—	—	—	—	—	—
Apr	—	14	1	—	—	—	—	—	—	—	—	—
May	—	2	—	4	5	—	—	—	—	—	—	—
Jun	—	—	4	4	3	—	4	1	—	2	1	1
Jul	3	5	—	1	—	1	—	—	1	—	—	1
Aug	14	6	—	—	—	—	—	—	—	—	1	—
Sep	3	6	—	—	—	—	—	—	—	—	—	—
Oct	3	11	—	—	—	—	—	—	—	—	—	—
Nov	—	2	—	—	—	—	—	—	—	—	—	—

reproductively capable individuals are present each month from April through mid-June. The subsequent sharp decrease in testis size and the absence of spermatozoa suggest that the majority of males copulate during June and early July. The gradual increase in overall testis size (Fig. 1), as well as the presence and proliferation of early germinal stages (spermatogonia and primary spermatocytes; Fig. 2), from August to October show that spermatogenesis resumes shortly after copulation. Ovarian follicles undergoing vitellogenic growth ( $\geq 2$  mm diameter) first appear in mid-April. Between April and July all females (but two) of adult size contained vitellogenic follicles (generally two per ovary) in both ovaries, indicating that virtually all adult females reproduce each season.

Moroccan and Spanish male *A. erythrurus* show similar cycles of reproductive maturation, evacuation of testes, and spermatogenesis. Based on changes in the mean number of spermatids and spermatozoa in the seminiferous tubules of individuals collected during a single breeding season, Bons (1969) suggested that individual males in Morocco experience two waves of sperm production per season. Histological examination does not confirm a similar phenomenon in males from Spain. Testes from a few individuals in our study did contain, in addition to cellular debris indicative of recent evacuation of spermatozoa, numerous primary spermatocytes in the seminiferous tubules. Whether these spermatocytes continue to develop into a second "wave" of spermatozoa in the same season, or simply degenerate, is unknown. The most notable difference between these two populations concerns the period during which reproductively mature males are present. This period is apparently shorter, but is followed by earlier resumption of spermatogenesis, in Spain.

Vitellogenesis and ovulation likewise occur over the same timespan in the two populations. Bons (1972) suggests two phases of vitellogenic growth during a single breeding season for larger female *A. erythrurus* in Morocco. Older (i.e. larger) females produce two clutches each year and younger individuals produce only one. Evidence for the production of two clutches during a single season can be inferred by: (1) simultaneous presence in an ovary of vitellogenic follicles of two distinct size classes, (2) asymmetrical vitellogenic growth of follicles between ovaries (as in allochronic ovulation [Jones, 1978]), or (3) the presence of young corpora lutea in addition to vitellogenic follicles. None of these conditions was observed during our study. While we cannot rule out the possibility that second

clutches are deposited by Spanish females, our data do not favor this hypothesis over one which infers reproduction over an extended period.

Mature females in Morocco lay between two and six eggs in early clutches, but second clutches contain only one to three eggs (Bons, 1962). In Spain, mature females may produce as many as five eggs, the average clutch size is three eggs, and there is no direct evidence for the production of multiple clutches. Thus the Moroccan population produces more and (sometimes) larger clutches per female than the Spanish population.

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## KARYOTYPIC ANALYSIS OF FIVE RODENTS AND A MARSUPIAL FROM BELIZE, CENTRAL AMERICA

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## ABSTRACT

Karyotypes and chromosomal banding patterns of six species of small mammals from Belize are presented and discussed in light of relevant data in the literature. Individuals of *Heteromys desmarestianus* had FN values of 72, which differs from previous reports. G-bands were obtained and compared to fluorescent bands (DAPI) and with the location of NOR sites. The karyotypes of *Peromyscus mexicanus*, *Sigmodon hispidus*, *Oryzomys couesi*, and *Ototylomys phyllotis* are identical to the karyotypes for these species described in the literature. Active NORs were located on four pairs of chromosomes in *O. phyllotis* and fluorescent bands obtained with the stain Hoechst 33258. The karyotype of *Marmosa robinsoni* appears similar to that described by Hsu and Benirschke (1971). Autosomal C-bands were located at the centromeres. The X had interstitial C-bands and the Y was entirely heterochromatic. Silver stained NORs were present on five chromosomes corresponding to chromosomal pairs 4, 5, and 6.

## INTRODUCTION

The small mammal fauna of Belize has not been extensively surveyed (Hershkovitz, 1951; Laurie, 1954). Kirkpatrick and Cartwright (1975) compiled a list of the mammals known to occur in Belize, but the list must be considered incomplete due to the limited amount of study the fauna has received. During the spring of 1983 the Section of Mammals, The Carnegie Museum of Natural History, conducted a collecting trip to obtain specimens, primarily of bats, rodents, and marsupials. This paper presents the findings of karyotypic analyses of six species of mammals collected throughout Belize.

## MATERIALS AND METHODS

All karyotypes were obtained from bone marrow preparations made in the field by the methods described by Patton (1967), Lee (1969), and Baker et al. (1982). Individuals to be karyotyped were usually injected with yeast to increase the mitotic index according to the methods of Lee and Elder (1979). Several slides were prepared in the field, with the remaining cell suspension frozen in liquid nitrogen to permit slide preparation in the lab. C-banding was performed on air dried slides by a modification of the technique of Stefos and Arrighi (1971). G-banding was accomplished using the

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technique of Seabright (1971). Nucleolus organizer regions (NORs) were located by the silver staining method of Gold and Ellison (1983). Fluorescent banding was done with the stains 4,6-diamidino-2-phenylindole (DAPI) and Hoechst 33258 as described by Disteché and Bontemps (1974), and Schweizer (1976), respectively. Fluorescent banding permits the identification of homologous chromosomes and identifies regions with specific DNA base composition. Hoechst 33258 and DAPI are specific for AT (adenine and thymine) rich regions and produce a banding pattern analogous to G-bands.

### SPECIMENS EXAMINED

All specimens were collected in Belize, Central America, and deposited in The Carnegie Museum of Natural History (CM).

*Heteromys desmarestianus*.—CM 91973, female, Stann Creek District, 7.0 km WNW Quam Bank, Cockscomb Basin; CM 91997, female, Toledo District, 1.8 km NNW Forestry Camp (Salamanca), Columbia Forest Reserve; CM 91988, male, Stann Creek District, 3.4 km WNW Quam Bank, Cockscomb Basin.

*Ototylomys phyllotis*.—CM 92020, male, CM 92014, female, Belize District, Altun Ha ruins; CM 92034, female, Toledo District, 0.7 km NNE Forestry Camp (Salamanca), Columbia Forest Reserve.

*Sigmodon hispidus*.—CM92082, female, Stann Creek District, Quam Bank, Airstrip, Cockscomb Basin.

*Oryzomys couesi*.—CM92005, female, Stann Creek District, Cabbage Haul Ridge, 2.8 km SSE Quam Bank, Cockscomb Basin.

*Peromyscus mexicanus*.—CM 92039, female, and CM 92037, male, Toledo District, Jimmy Cut 2.1 km NW Forestry Camp (Salamanca), Columbia Forest Reserve.

*Marmosa robinsoni*.—CM91638, male, Toledo District, 2.1 km N Forestry Camp (Salamanca), Columbia Forest Reserve.

### RESULTS AND DISCUSSION

#### *Heteromys desmarestianus* ( $2n = 60$ , $FN = 72$ )

The karyotype presented in Fig. 1a shows chromosomes 1, 2, 4, and 5 are large and subtelocentric and chromosome 3 is large and submetacentric. There are 22 acrocentric pairs that grade in size from large to small, and two pairs of small metacentric autosomes. The X chromosome is medium-sized and metacentric. Fig. 1b and 1c display the G-bands and fluorescent bands obtained with DAPI, respectively. It appears that the centromeric regions are not A-T rich and that dark G-bands correspond to bright regions with DAPI as expected. Fig. 1d shows active NOR sites on at least six pairs of autosomes. Genoways (1973) and Engstrom et al. (in press) report  $2n = 60$ ,  $FN = 82$  and  $2n = 60$ ,  $FN = 66$ , respectively, for *H. desmarestianus*. Thus, variation in fundamental number is extensive within this species.

#### *Ototylomys phyllotis* ( $2n = 48$ , $FN = 78$ )

The big-eared climbing rat is found throughout the Yucatan Peninsula and south through Belize, Guatemala, Honduras, El Salvador, Nicaragua, and the northern half of Costa Rica (Hall, 1981). Lawlor (1969) recognized three subspecies, which are separated altitudinally. *Ototylomys* is most closely related morphologically to *Tylomys* and is allied to *Neotoma* by similarities of the accessory reproductive glands (Lawlor, 1969). The nondifferentially stained karyotype, presented in Fig. 2a, contains one pair of large submetacentric, three pairs of large metacentric, one pair of large acrocentric, one pair of medium-sized submetacentric, one pair of medium-sized acrocentric, five pairs of medium-sized metacentric, six pairs of small metacentric and five pairs of small acrocentric autosomes. The X and Y are large and metacentric. The karyotype of *O. phyllotis* reported here is identical to the nondifferentially stained karyotype originally reported by Hsu and Benirschke (1973). Fig. 2b shows a spread stained with the

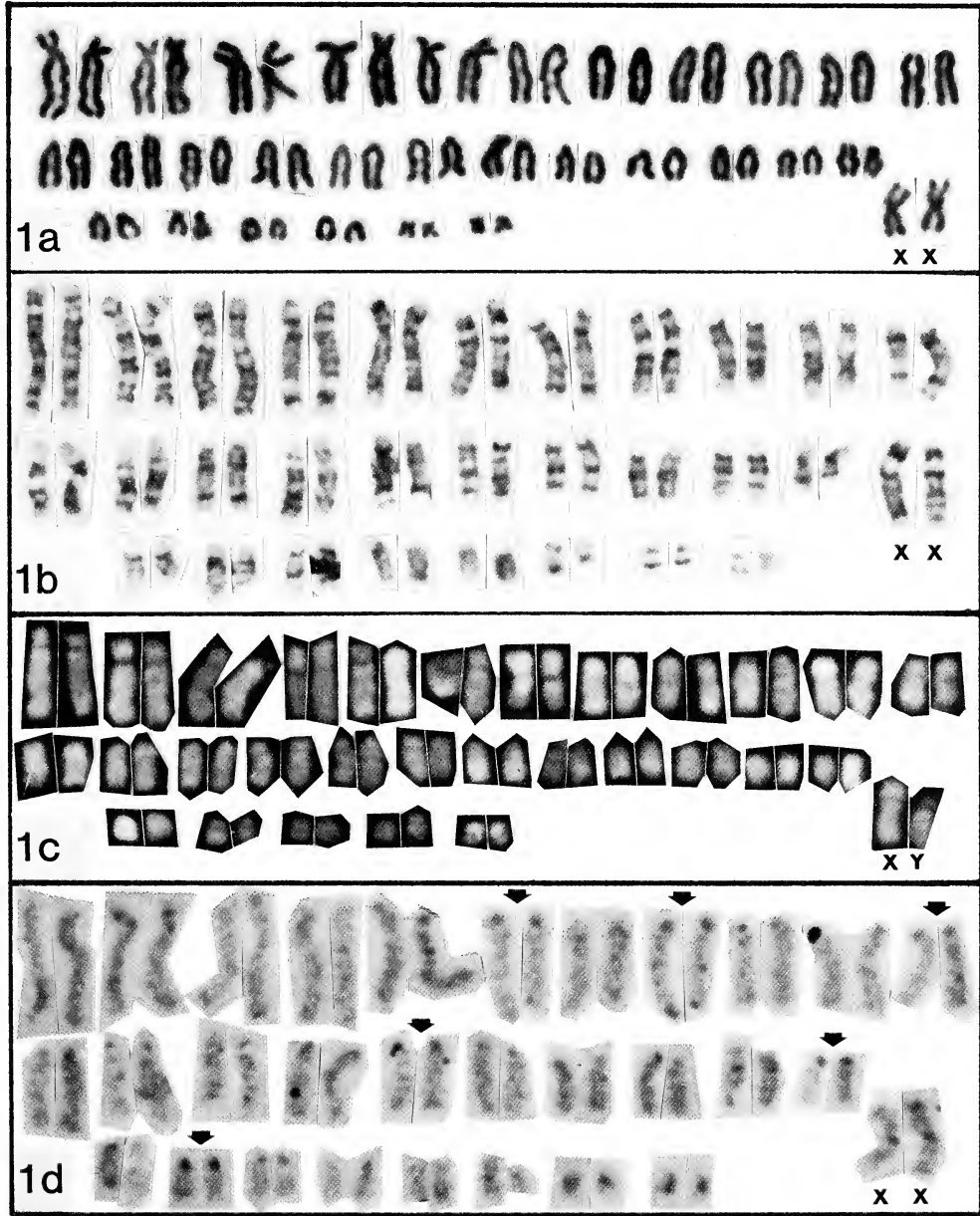


Fig. 1.—a) Nondifferentially stained karyotype of *Heteromys desmarestianus*. b) G-banded karyotype. c) DAPI stained karyotype. d) Silver-stained NOR sites.

fluorescent dye Hoechst 33258. The banding pattern indicates that much of the X chromosome is AT rich but not the centromere. Active NORs (Fig. 2c) are present on one pair of small acrocentric and three pairs of medium-sized meta-centric autosomes.



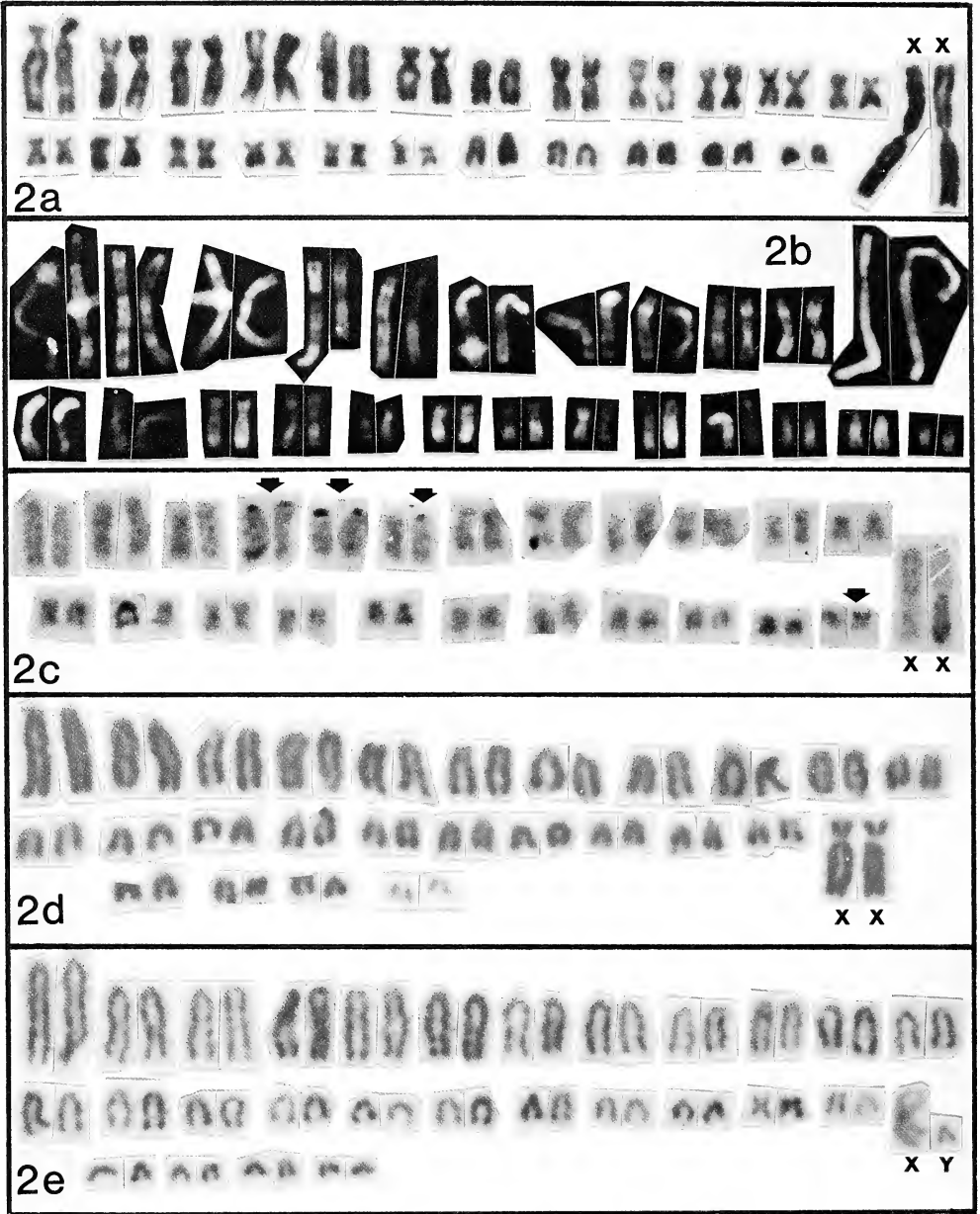


Fig. 2.—a) Nondifferentially stained karyotype of *Ototylomys phyllotis*. b) Karyotype stained with Hoechst 33258. c) Silver stained NOR sites. *O. phyllotis*. d) Nondifferentially stained karyotype of *Sigmodon hispidus*. e) Nondifferentially stained karyotype of *Oryzomys palustris*.

*Sigmodon hispidus* ( $2n = 52$ ,  $FN = 52$ )

The karyotype presented in Fig. 2d contains 48 acrocentric and two very small metacentric autosomes. The X chromosome is large and subtelocentric and the Y small and metacentric. This karyotype is identical to that described by Zim-



merman (1970) and Kiblsky (1969) who stated this karyotype is found from the eastern United States to Venezuela.

Elder (1980) studied chromosomal evolution in the genus *Sigmodon* and found that two morphologically similar but karyotypically different species, *S. arizonae* ( $2n = 22$ ,  $24$ ,  $FN = 38$ ) and *S. mascotensis* ( $2n = 28$ ,  $FN = 29$ ), share a high degree of G-band homology. Chromosomal evolution in the genus has been toward lower diploid numbers by the rearrangement events of tandem and centric fusion.

*Oryzomys couesi* ( $2n = 56$ ,  $FN = 56$ )

The karyotype presented in Fig. 2e is identical to that reported by Benson and Gehlbach (1979) and Haiduk et al. (1979) for *O. couesi*. There are 26 pairs of acrocentric and one small pair of metacentric autosomes. The X is large and submetacentric and the Y, as reported by Haiduk et al. (1979), is small and subtelocentric.

Honacki et al. (1982) list over 50 species of *Oryzomys* ranging from South America to the eastern United States making this one of the most complex mammalian genera. Diploid numbers within the genus range from 52 to 80 and possess FNs from 62 to 112 (Gardner and Patton, 1976). Haiduk et al. (1979) observed extensive G-band differences between *O. melanotis* and *O. palustris*, which possess very similar nondifferentially stained karyotypes, and concluded that karyotypic evolution in *Oryzomys* is very rapid compared to other vertebrates. The analysis of G-banding patterns by Baker et al. (1983) found that current models of chromosomal evolution do not adequately explain the variation found within and between the peromyscine-neotomine-oryzomine lineages.

*Peromyscus mexicanus* ( $2n = 48$ ,  $FN = 58$ )

Chromosomal banding patterns have been studied for 12 species of the *Peromyscus mexicanus* group (Robbins and Baker, 1981; Rogers et al., 1984; Stangl and Baker, 1984; Smith et al., 1986). These species possess a high degree of karyotypic conservatism, which is unusual for the genus. The karyotypes of members of the *P. mexicanus* group are characterized by having  $2n = 48$  and  $FN = 58$  with biarmed chromosomes 1–3, 9, 22, and 23. Seven members of the *P. mexicanus* group have been described as having heterochromatin restricted to the centrometric regions (Huckaby, 1980; Rogers et al., 1984; Stangl and Baker, 1984).

Smith et al. (1986) state that there is a considerable amount of variation in the morphology of the X chromosome within the *P. mexicanus* group. They list seven species with submetacentric and two species with nearly acrocentric X chromosomes, and state that the differences are caused by heterochromatic short arm variations. The Y chromosome in members of the *P. mexicanus* group are either biarmed or acrocentric (Smith et al., 1986). Rogers et al. (1984) and Smith et al. (1986) conclude that the *P. mexicanus* karyotype does not represent the primitive autosomal karyotype for the genus, but is an intermediate form that has stabilized relative to more highly derived karyotypes, possibly due to selective forces.

The karyotype of *P. mexicanus* presented in Fig. 3a has the autosomal complement typical of *P. mexicanus*, but the Y chromosome seems to be considerably smaller. The G-band pattern (Fig. 3b) of the autosomal complement is generally similar to that of other members of *P. mexicanus*. This includes biarmed autosomes 1–3, 9, 22, and 23 and acrocentric autosomes 4–8 and 10–21. The G-band

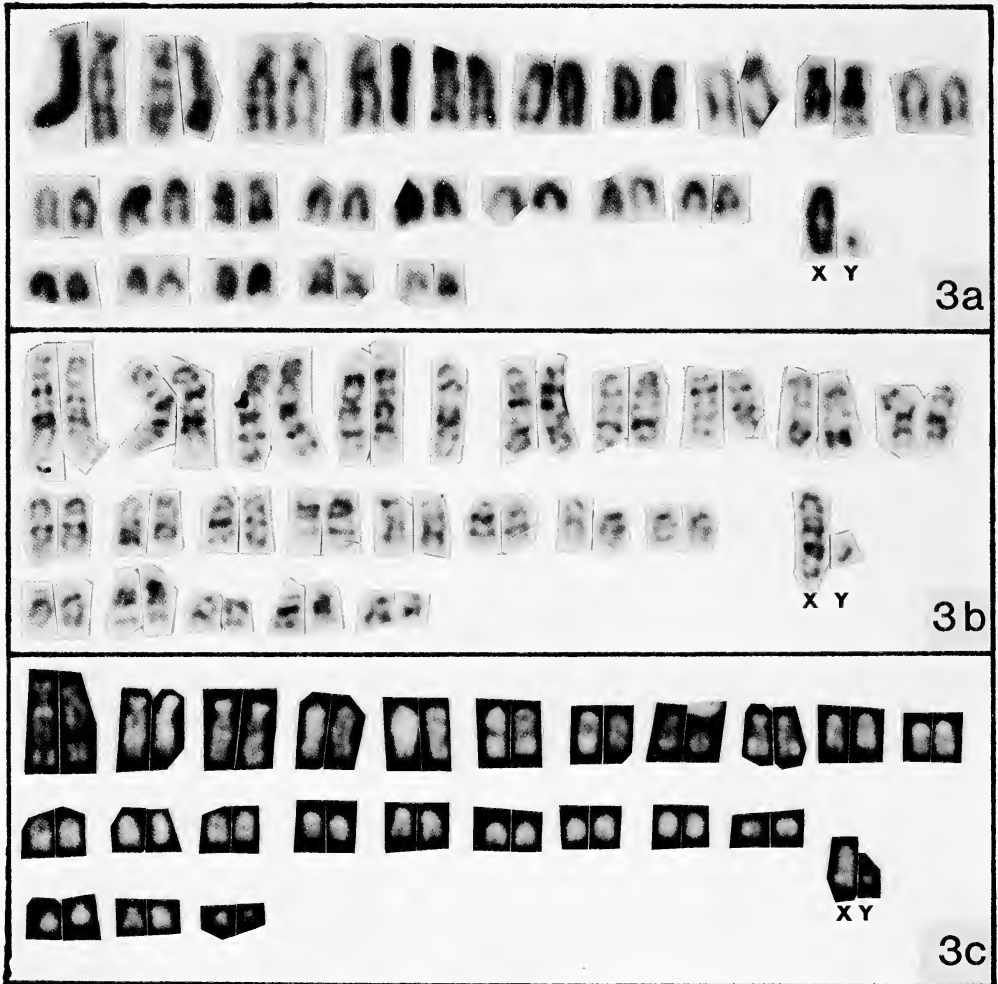


Fig. 3.—a) Nondifferentially stained karyotype of *Peromyscus mexicanus*. b) G-banded karyotype of *P. mexicanus*, homolog to chromosome five missing. c) DAPI stained karyotype of *P. mexicanus*.

chromosomes (Fig. 3b) are placed in numerical order (decreasing size) and identified according to the nomenclature of Committee (1977).

The banding pattern obtained with the fluorescent stain Hoechst 33258 is shown in Fig. 3c. This stain indicates that the centromeric heterochromatin in *P. mexicanus* is not particularly AT rich. Chromosome 1 contains bright regions at the end of both the long and short arms and in the area directly below the centromeric region. Chromosomes 2 and 3 also contain bright interstitial bands. Chromosomes 4 through 12 often have bright regions at the ends of the long arms and may also have bright centromeric bands. The small acrocentric chromosomes of *P. mexicanus* appear to be bright primarily in their centromeric regions, and dark distally.

*Marmosa robinsoni* ( $2n = 14$ ,  $FN = 24$ )

There is considerable information on the nonbanded karyotypes of marsupials (see Hayman's 1977 review), however, there are only a few papers (Curcuro-

Giordano et al., 1974; Fernandes-Donoso et al., 1979; Merry et al., 1983; Seluja et al., 1984; Sinha and Kakati, 1976; Sinha et al., 1972; Yonenaga-Yassuda et al., 1982) that present banded karyotypes. The reason that more species have not been examined is that it is difficult to obtain quality preparations with marsupial chromosomes (Seluja et al., 1984). Marsupials have a slow rate of karyotypic evolution. Previous studies have revealed only three different diploid numbers,  $2n = 14, 18, 22$  (Hayman, 1977). Sharman (1961) hypothesized that the evolution of the Australian marsupials may have been associated with reduction in the number of chromosomes. This hypothesis also has been considered to apply to the evolution of American marsupials (Sharman, 1973, 1974; Reig et al., 1977).

The karyotypes of the  $2n = 14$  American didelphids are all very similar with only minor differences between species representing different subfamilies (Reig et al., 1977). Hayman (1977) felt that the possibility existed that the standard non-banded karyotype would not separate some species and that banding techniques would be required for karyotypic identification.

The murine opossums (*Marmosa*) are the most diverse Neotropical marsupials, but of the 37 recognized species almost nothing is known about them karyotypically (Reig, 1970). There are only three "mouse" opossums known to occur in the country of Belize (Kirkpatrick and Cartwright, 1975), these are *Marmosa alstoni*, *M. robinsoni*, and *M. mexicanus*. Curcuro-Giordano et al. (1974) obtained Q-bands on *M. mitis*, a junior synonym for *M. robinsoni* (O'Connell, 1983) and were able to identify every homologous pair of chromosomes. Fernandes-Donoso et al. (1979) reported the location of NORs in *M. elegans*; no other member of the genus *Marmosa* has been studied for banded karyotypes.

Nondifferentially stained karyotypes have been obtained from eight species of *Marmosa* and three species of *Caluromys* (Reig, 1968; Reig et al., 1977; Biggers et al., 1965; Hsu and Benirschke, 1971). All were found to have  $2n = 14$  and  $FN = 24$ . Nearly all have the same proportions (1:3:2) of metacentric, submetacentric, and subtelocentric chromosomes, with the only two exceptions being *M. elegans* with only one subtelocentric and a single acrocentric, and *M. fuscata* with four submetacentric and no subtelocentric chromosomes (Reig et al., 1977). Reig (1970) pointed out that the similarities are noteworthy because *Marmosa* and *Caluromys* are considered to be in different subfamilies of the didelphids. He stated that the differences between the karyotypes of other genera in the Didelphinae and *Marmosa* are greater than the differences between *Caluromys* and *Marmosa* and that the first four pairs of autosomes of *M. fuscata*, *M. robinsoni* and *C. derbianus* are indistinguishable.

The morphology of the X chromosome ranges from acrocentric in *C. derbianus*, *C. lanatus*, and *M. alstoni*, to subtelocentric in *C. philander*, *M. elegans*, and *M. robinsoni*, to metacentric in *M. murina*, *M. pusilla*, and *M. cinerea*. The Y chromosome is acrocentric in all these species (Reig et al., 1977).

In this paper we report on the Ag-NOR sites and C-bands of *M. robinsoni*. The nondifferentially stained karyotype of our specimen is the same as that described by Hsu and Benirschke (1971). C-bands are presented in Fig. 4a and show heterochromatin in the autosomes to be confined to the centromeric regions. The Y chromosome is entirely heterochromatic, and the X appears to have two interstitial C-bands. NORs are shown in Fig. 4b and are present on chromosomes 4, 5, and 6.

Centromeric heterochromatin has also been found in the autosomes of *Philander opossum*, *Didelphis albiventris* (Yonenaga-Yassuda et al., 1982; Seluja et al., 1984), and *Monodelphis domestica* (Merry et al., 1983). The X chromosome of *P.*

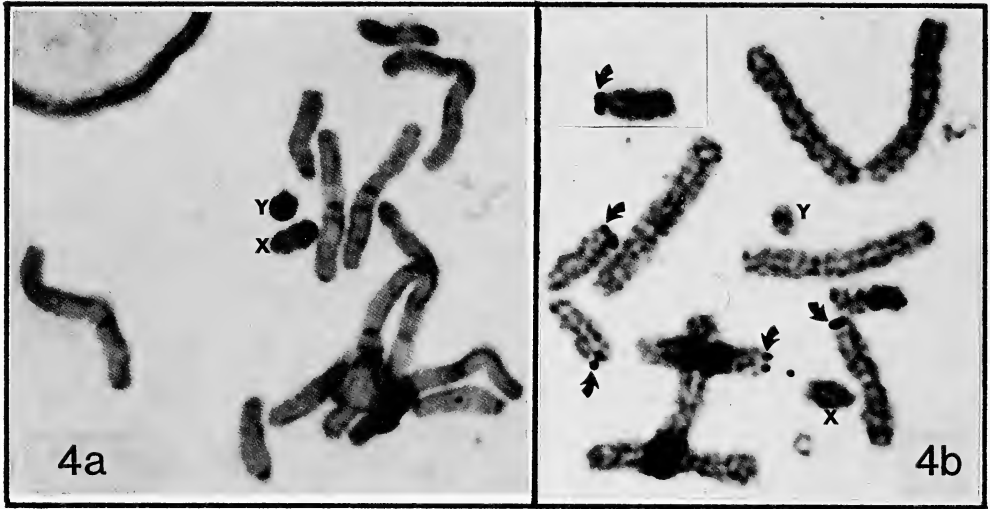


Fig. 4.—a) C-banded spread of *Marmosa robinsoni*. b) Silver stained NOR sites (arrows).

*opossum* has a single band in the long arm and a completely heterochromatic Y chromosome. In *Didelphis albiventris* the X chromosome has a centromeric band. Both *D. marsupialis* and *Lutreolina crassicaudata* lack centromeric heterochromatin on the autosomes but possess C-band positive material on the X chromosomes. The Y chromosomes of both these species are totally heterochromatic (Seluja et al., 1984).

Nucleolar organizer regions (NORs) have been studied in only one other member of the genus *Marmosa*. In *M. elegans* NORs were located at secondary constrictions on the short arm of a single autosomal pair (Fernandes-Donoso et al., 1979). A few studies on the distribution of NORs have been published for several other species of marsupials. Seluja et al. (1984) found NORs located on chromosome pairs 4, 5, and 6 in *Didelphis albiventris* and on the short arm of chromosome pair 5 and the long arm of chromosome pair 7 in *Lutreolina crassicaudata*. In *D. marsupialis* the NORs were terminally located in the long arms of two pairs and in the short arm of one other pair. The NOR bearing chromosomes could not be specifically identified, but there were specimens with up to eight active NORs and as few as four (Yonenaga-Yassuda et al., 1982). In *P. opossum* the NORs were located terminally in the short arm of pair 5 and the long arm of pair 7 (Yonenaga-Yassuda et al., 1982). NOR bearing sex chromosomes have been found in *Potorous tridactylis* (Goodpasture and Bloom, 1975), *Lagorchestes conspicillatus* (Hayman and Sharp, 1981), *Trichosurus vulpecula* (Murray, 1977), and in *Monodelphis domestica* (Merry et al., 1983).

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BIOSYSTEMATIC STUDIES IN *STENANTHIUM*  
(LILIACEAE: VERATREAE).I. FLORAL MORPHOLOGY, FLORAL VASCULAR ANATOMY,  
GEOGRAPHY AND TAXONOMY OF *S. OCCIDENTALE* A. GRAY

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## ABSTRACT

The floral morphology, continuous pedicel to stigma floral vascularization, distribution and lectotypification of *Stenanthium occidentale*, a western North American bulbous lily, are presented. The perfect, protandrous flowers with dimorphic filaments and bilobed or v-shaped tepal nectaries which promote outbreeding are arranged in andromonoecious racemes. Raphide idioblasts were not observed. Total floral vascularization is derived from three lower pedicel bundles. A spiral series of divisions and fusions in the upper pedicel produces three compound outer tepal and three compound inner tepal bundles. From the former, an outer tepal median, outer tepal laterals, an outer stamen and a dorsal bundle result, while from the latter, an inner tepal median, inner tepal laterals and an inner stamen bundle result. Their formation is above that at which the ventral and ovular supplies are established due to an inferior gynoecium with a central carpellary hole and epigynous perianth. The ventral supply is spirally derived from continuing bundles following the formation of the compound inner tepal bundles. Within each septal arm, a shared septal axial is associated with but remains free of a compound ventral that divides into two ventrals. The bitegmic, basitropic, campylotropous ovules develop into flat, oblong, winged seeds.

## INTRODUCTION

This is the first of several papers which will discuss the biosystematics of the genus *Stenanthium* Kunth (1842), a conserved generic name (Farr et al., 1979; Voss, 1983). The four currently recognized species of *Stenanthium*, which are *S. occidentale* A. Gray, *S. frigidum* (Schlecht. & Cham.) Kunth, *S. gramineum* (Ker-Gawl) Kunth (including *S. robustum* S. Watson) and *S. sachalinense* F. Schmidt, have traditionally and consistently been placed in the Liliaceae, subfamily Melanthioideae, tribe Veratreae (Bentham and Hooker, 1883; Engler, 1889; Gates, 1918; Krause, 1930; Zimmerman, 1958; Kupchan et al., 1961; Melchior, 1964; Hutchinson, 1973; Schulze, 1978; Dahlgren et al., 1985).

This paper presents the floral morphology, floral vascular anatomy, distribution and taxonomy of *S. occidentale*. Several common names have been used for this species—"western *Stenanthium*" (Carter and Newcombe, 1921; Abrams, 1940; Peck, 1941; Brockman, 1947; Hitchcock and Cronquist, 1973; Ferlatte, 1974), "bronze bells" (Carter and Newcombe, 1921; Moss, 1959; Larrison et al., 1974; Clark, 1976; Kuijt, 1982), and "mountain bells" (St. John and Hardin, 1929; Clark, 1976; Taylor and MacBryde, 1977; Scoggan, 1978), in reference to its western location and greenish brown, narrowly campanulate flowers.

## MATERIALS AND METHODS

Three different populations of *Stenanthium occidentale* were studied in western North America—Oregon: Lane County, Willamette National Forest, Walker Creek, Lowder Mountain, 5 July 1978,

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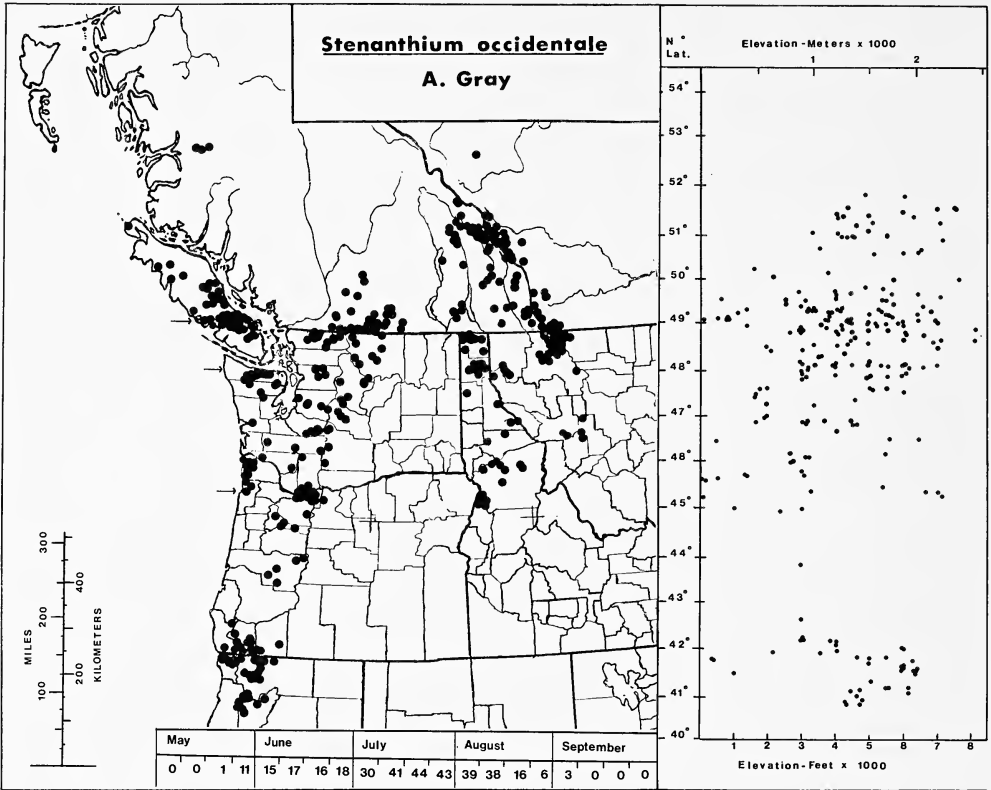


Fig. 1.—Distribution and elevation of *Stenanthium occidentale* A. Gray based on herbarium specimens. Arrows indicate regions where the range approaches sea level. Flowering frequency is summarized by week and month.

*Utech* 78-275 (CM); Washington: Lewis County, Mt. Rainier National Park, Silver Falls, near Stevens Canyon, 7 July 1977, *Utech* 77-201 (CM); Washington: Whatcom County, Mt. Baker National Forest, Austin Pass, 11 July 1978, *Utech* 78-300 (CM). Herbarium collections examined are cited in the taxonomy review.

Flowering inflorescences of varying age collected from the three study sites were fixed in acetic-ethanol (1:3) for 10 hours with subsequent storage in 70% ethanol. Standardized transverse and longitudinal paraffin sectioning (14–16  $\mu$ ) and staining (saffarin-methylene blue) techniques (Johansen, 1940; Sass, 1958) were used on floral samples of varying stages from all three populations. As an additional check on these sections, whole flowers were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

Distribution based on herbarium specimens (Fig. 1) and various aspects of floral morphometrics (Fig. 3, 4) are presented. Composite photomicrographs (Fig. 5–9) present the vascular floral anatomy and morphology of *S. occidentale*, whereas Fig. 10 is a summary floral vascularization diagram. No teleological implications are intended in the descriptive ascent and departure of the various floral bundles and traces which are letter-coded for ease in comparison. This coding parallels that used in our previous liliaceous studies (Utech, 1978a, 1978b, 1978c, 1978d, 1978e, 1979a, 1979b, 1982, 1984, 1986; Utech and Kawano, 1975, 1976, 1980, 1981), but it does not imply homology.

## OBSERVATIONS

### *Morphology and Floral Vascular Anatomy*

*Stenanthium occidentale* is a glabrous perennial with narrowly ovoid, tunicated bulbs (1.0) 1.5–3.5 cm long, and 2–4 mostly basal, linear to narrowly oblanceolate



Table 1.—*Degree of inflorescence branching in Stenanthium occidentale based on herbarium collections and field study plots (2 × 2 meter).*

Material	Branch points within inflorescence									
	0		1		2		3		Total	
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
Herbarium collections	796	(75.4)	219	(20.7)	39	(3.7)	2	(0.2)	1056	(100)
<i>Utech 78-275</i>	152	(73.1)	40	(19.2)	16	(7.7)	0	—	208	(100)
<i>Utech 77-201</i>	135	(77.1)	33	(18.9)	7	(4.0)	0	—	175	(100)
<i>Utech 78-300</i>	210	(71.4)	62	(21.1)	21	(7.2)	1	(0.3)	294	(100)

leaves (10) 15–30 cm long, 5–20 (25) mm wide. The basal leaves are lax, gradually narrowed at both ends, and sheathing at their bases. The weak, erect and usually simple stems measure (2.5) 3.0–4.5 (6.0) dm in length. The few stem leaves are progressively reduced apically.

The floral portion of an unbranched inflorescence typically measures 1.0–2.0 dm long. Occasionally on larger plants, there are floral branches at the lower nodes. When a second, rarely a third, branch occurs, a simple panicle or compound raceme results (Fig. 3, 11; Table 1). Each pedicel irrespective of the degree of branching is associated with a scarious lanceolate bract which measures 6–10 mm at the lower nodes and is progressively shorter upwards (Fig. 2). The total number of flowers per plant varies from 7 to 30 depending on the degree of branching (Fig. 3; Table 1). Without branching, the average flower number is 10 in a simple raceme, and with one branch point, the average increases to 14 flowers in a simple panicle. The typical raceme is weakly andromonoecious due to a declining array of protandrous flowers. Beginning at the base, most flowers do set fruit. Floral phenology lasts for a relatively long time period, based on the number of flowers present and their flowering sequence. From both field observations and herbarium collections, the average plant size appears to be directly proportional to the total number of flowers, seeds, or fruits produced (Fig. 3).

The flowering pedicels are normally 7–17 mm long with pendulous flowers (Fig. 2A–C, 4). In fruit, on the other hand, the pedicels are elongated and ascending with upright fruit (Fig. 2D, 4). Flowering and fruiting pedicels have the same number of bundles and vascular arrangement and differ only in that the latter is longer and has a sclerenchymatous sheath surrounding the central bundles. In cross-section, the lower pedicels are generally circular with three large, centrally arranged bundles. These three bundles establish the complete floral vasculature (Fig. 10) and are located on radii which are designated the outer tepal (OT) radii. The three radii between the OT radii are designated the inner tepal (IT) radii.

Each of the three lower pedicel bundles along the OT radii undergoes a tri-parted, radial division with three resulting bundles. However, these tri-parted divisions occur at slightly different levels, that is, they are not co-planar, but rather follow a spiral pattern. A gap is created by the outward departure of the central bundle product of each tri-parted division. The three central bundles which depart along OT radii are designated the compound outer tepal or OT bundles (dorsal-compound bundle; Sterling, 1982). They remain free of other vasculature and eventually establish the outer tepal median (OTM), outer tepal lateral (OTL), outer stamen (OS) and dorsal (D) vasculature (Fig. 7D, E, 8, 10).

The two remaining lateral products adjoining a gap following a tri-parted division fuse with similar adjacent laterals along the IT radii (Fig. 10). These new

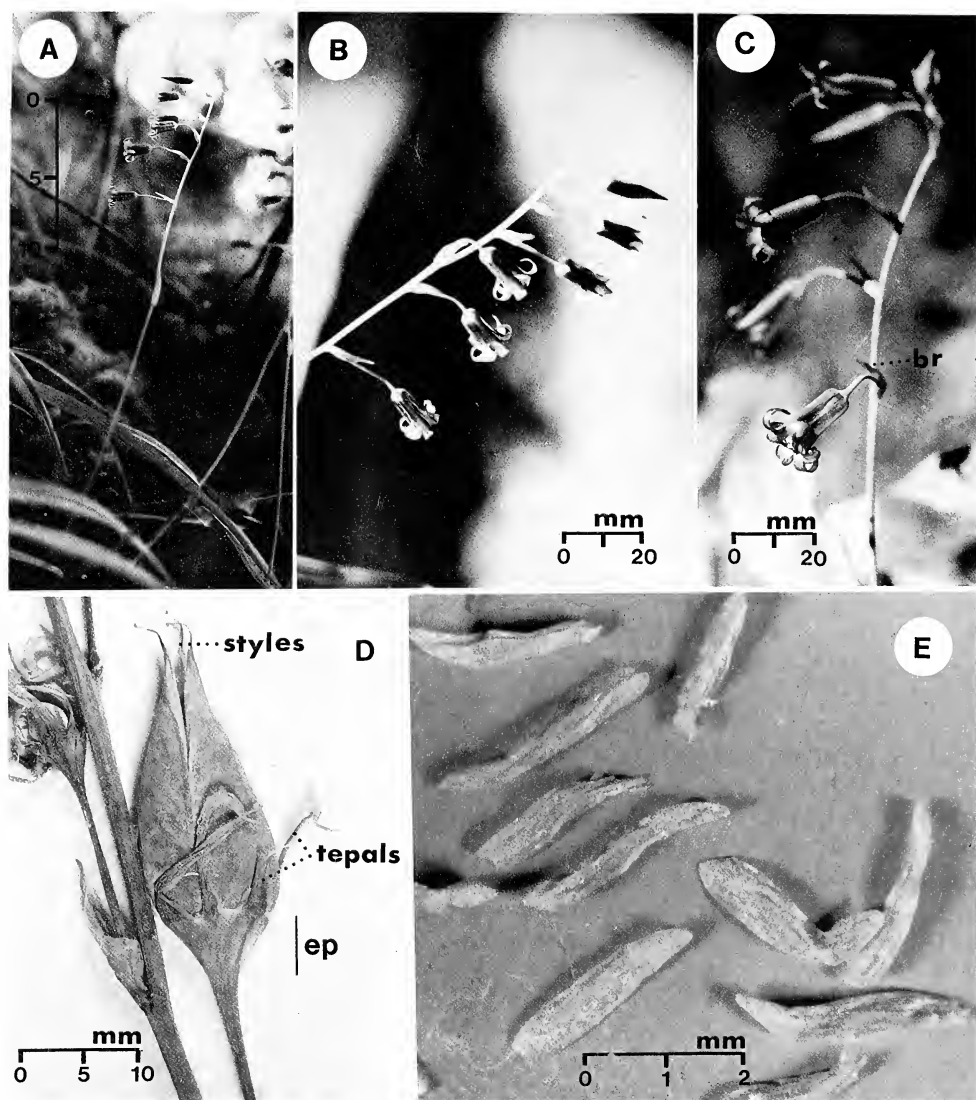


Fig. 2.—Flowering habit, fruit and seeds of *S. occidentale*. A–C. Three different views of simple flowering racemes, bracts (br) and nodding flowers. D. Mature fruit on an erect pedicel. The lower epigynous zone (ep) with persistent tepals, freed styles and zones of septicidal separation are evident. E. Flat, narrowly oblong, winged seeds.

fusion bundles are formed at progressively higher levels in a spiral pattern. Each of these three fusion fundles undergoes a tri-parted division similar to that observed at a lower level among the three original bundles. The central bundle products of this second set of tri-parted divisions depart along the IT radii and establish the compound inner tepal or IT bundles (“zwischenbündel”; Sterling, 1982).

Subsequent divisions among the compound OT and IT bundles will be discussed later. However, it should be stressed that their formation was in a spiral pattern.

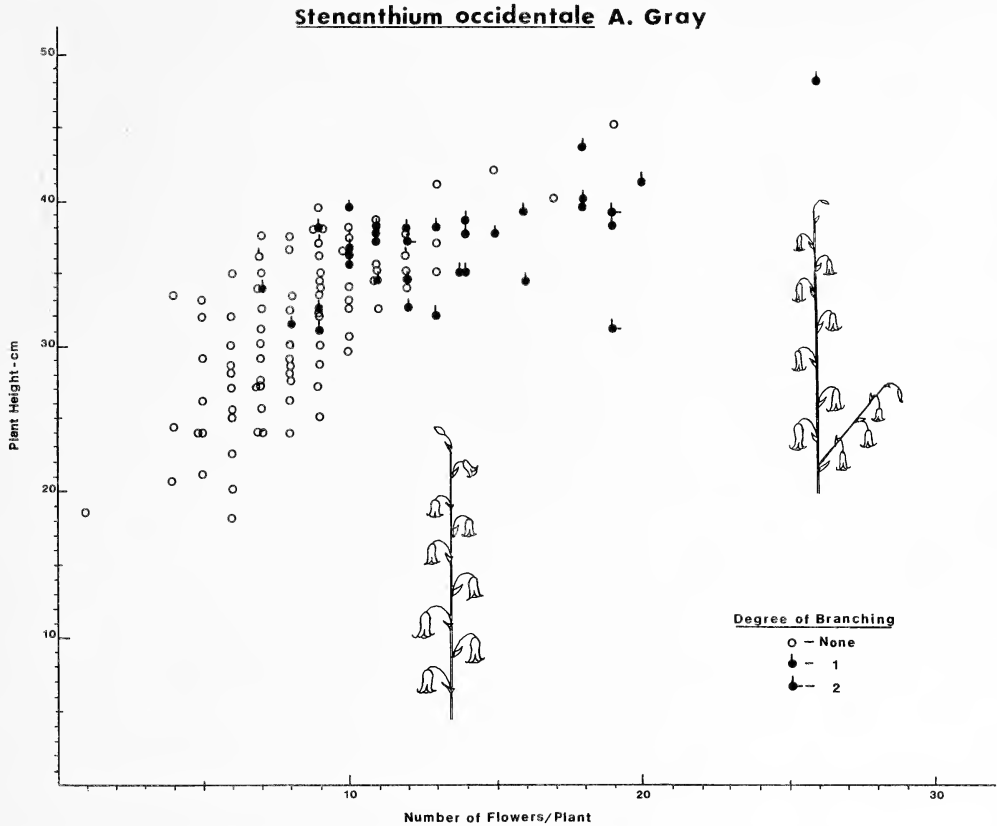


Fig. 3.—Scatter diagram comparing plant height (cm), number of flowers/plant and degree of inflorescence branching of *S. occidentale*. Each dot represents an individual plant selected randomly from range-wide herbarium specimens. Average inflorescence models are indicated for unbranched and branched plants. (Sample size: N = 120.)

A given pedicel cross-section will usually show one bundle departing, another being formed and a gap in an area where a third will be formed (Fig. 5B, C, 10).

The two remaining lateral bundles of the second, above mentioned tri-parted divisions fuse laterally with adjacent laterals. These three fusion products close the gaps along the OT radii which were formed when the compound OT bundles were established and departed. These three new fusion bundles establish the total ventral supply network of the gynoecium (Fig. 10). Dorsal formation is not associated with these bundles. These new bundles along OT radii undergo radial divisions at progressively higher levels. The two resulting products of each division fuse laterally with a similar adjacent lateral. Three new fusion bundles result along the IT radii. These bundles in turn close the gaps formed during the departure of the compound IT bundles. The three newly formed fusion bundles which are along the IT radii form the points of a central, triangular vascular zone ("stele").

The inferior gynoecium (Fig. 2D, 4) and its associated vasculature can best be described in two parts: that of the lower epigynous zone and that of the upper freed zone. Formation of the ventral supply, locule opening, ovule placentation and gynoecium subdivision all occur within the lower epigynous zone (Fig. 5B—

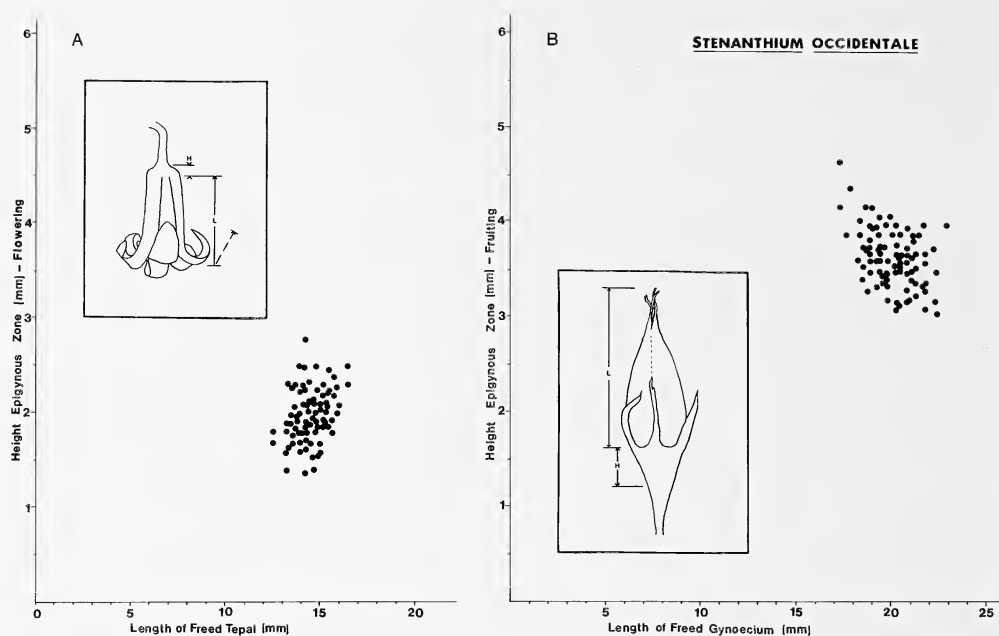


Fig. 4.—Floral scatter diagrams for *S. occidentale*. A. Comparison between freed tepal length (L in mm) to the height (H) of the flowering epigynous zone (mm). B. Comparison between the length (L) of the freed gynoecium (mm) to the height (H) of the epigynous zone (mm). While the epigynous zone height nearly doubles from the nodding flowering condition to that of the erect fruiting condition, the fruit appears only weakly inferior. The degree of epigyny is approximately 16% in fruit.

F, 6, 7A, B) in a spiral, not co-planar, pattern. The dorsal bundles which are derived from compound OT bundles are not established until the upper peripheral limits of the epigynous zone.

Following the formation and departure of the compound OT and compound IT bundles, a triangular vascular zone remains in the central area (Fig. 5D–F, 6A–D). The three large bundles which lie along the IT radii establish the triangle's corners and close the gaps formed by compound IT bundle departure (Fig. 6A–E). These three bundles designated as septal axials (SA) are formed at slightly different levels. The three locules open perpendicular to OT radii once the three corner bundles are established (Fig. 5D–F, 6). Also at this level, a central opening or “hole” appears (Fig. 7A, B) which indicates that the three locules will be interconnected along OT radii and three septal arms or wings freed along IT radii. The lower carpellary hole is internally continuous with the three locules and along the floral axis into the upper styler canal.

The three dorsals (D) are the last carpellary bundles to be formed in the upper epigynous zone. Furthermore, as the outer carpellary walls are freed from the surrounding perianth, the septal arms are subdivided internally along the IT radii (Fig. 7A, B). Septal glands were not observed. The three septal axials (SA) end in this zone without any further connection to the central ventral supply. The three carpels are freed from one another (Fig. 7) in what can best be described as a weakly appressed apocarpous condition. Each freed carpel has a dorsal (D) and two ventrals (V) which continue into the styler zone. There is no terminal carpellary fusion between the ventrals or between the ventrals and the dorsal. The

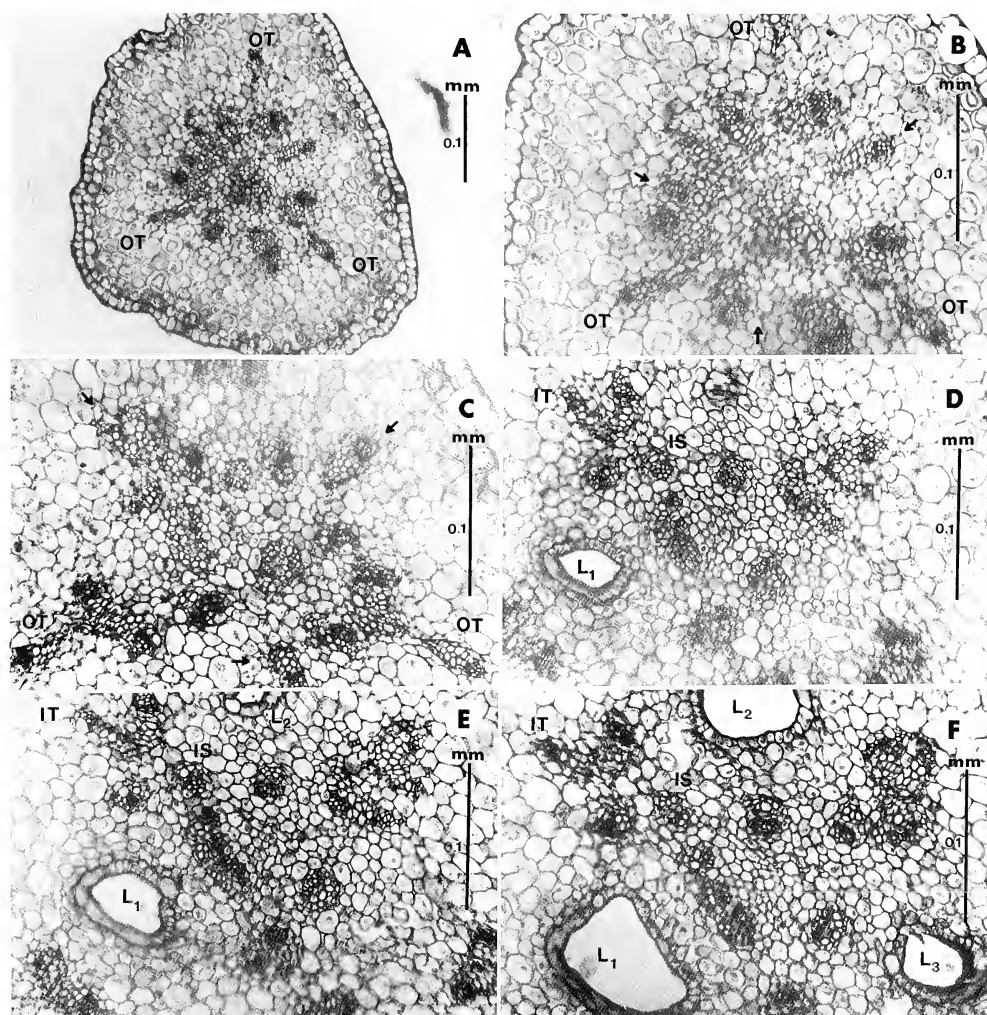


Fig. 5.—Transverse sections through the upper pedicel and lower receptacle of *S. occidentale* showing the formation and departure of both compound outer tepal (OT) bundle and compound inner tepal (IT) bundle as well as spiral locule opening. A. Mid-pedicel section showing the departure of three compound OT bundles. B. Enlargement of A detailing the progressive formation of three compound IT bundles (arrows). C. Upper pedicel section above B showing compound OT bundle departure and further formation of compound IT bundles (arrows). D. Section above C showing transition zone vascularization between the upper pedicel and lower receptacle. With first locule (L) opening and outward departure of compound OT and IT bundles, the remaining central bundles establish the ventral supply. E. Section above D with two open locules. F. Section above E showing three open locules. Formation of the ventral supply occurs in the central placental area before the dorsal supply is established.

stylar canal formed by the septal wing tips are lined with non-papillate cells. Each free upper style forms a stylodium (Fig. 2D). Raphide idioblasts were not observed in either carpellary or perianth tissue.

Each of the three carpels usually has eight to twelve bitegmic, basitropic, campylotropous ovules. The placental (P) bundles supplying these ovules depart quite

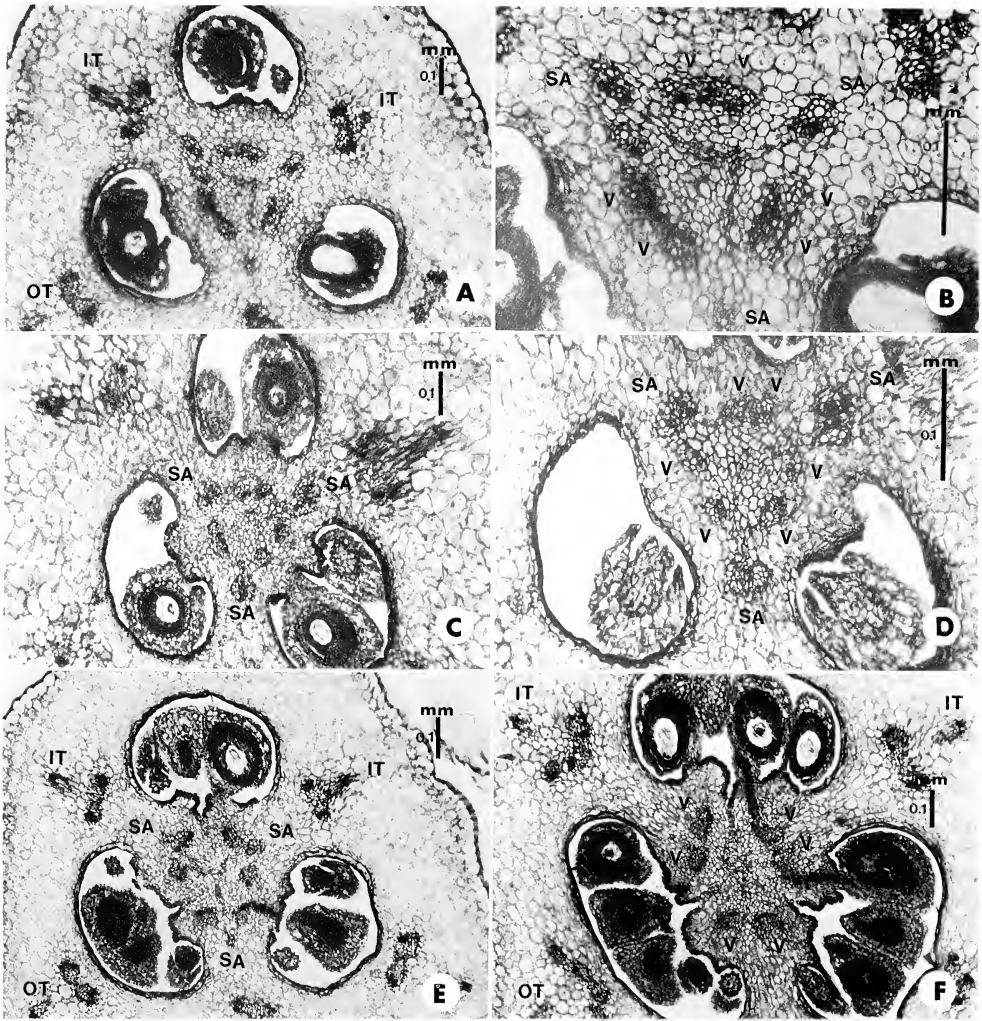


Fig. 6.—Transverse sections through the lower receptacle to upper epigynous zone of *S. occidentale*. A. Overview section showing the peripheral compound OT and IT bundles, the central ventral supply and ovules in all locules. B. Enlargement of A detailing the ventral supply. A pair of ventrals (V) is associated with each locule and a septal axial (SA) with each septal arm. C. Section above B showing ovular attachment. D. Enlargement of section above C detailing the ventral supply, compare with B. E. Overview section above D showing compound OT and IT bundles in outer epigynous zone and septal arm formation with simple septal axials (SA). F. Section above E showing further central zone subdivision and septal arm formation. Each carpel usually has four rows of ovules supplied via two ventrals (V). The dorsal supply is not established at this level.

horizontally in two ranks from a given ventral (V) (Fig. 6E, F, 7A, B, 10). Four rows of ovules per carpel are typical. Several flat, oblong, winged seeds are usually found in each carpel (Fig. 2D, E). The seed's distal appendage is directed upwards and away from its attachment point. Following anthesis, the gynoecium far surpasses the withered, persistent perianth and greatly reduces the observable floral epigyny and the semi-inferior gynoecium. Septicidal dehiscence begins in the free



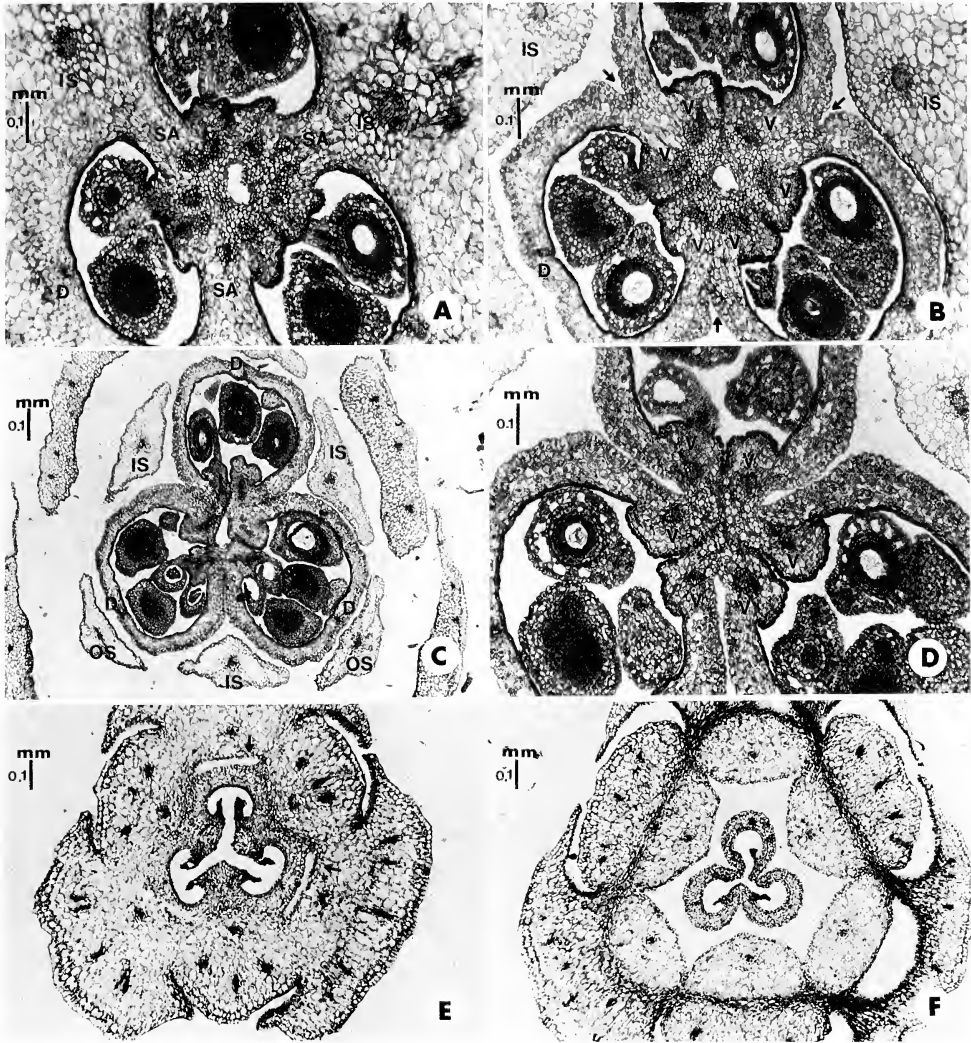


Fig. 7.—Transverse sections through the upper epigynous and freed carpellary zones of *S. occidentale* showing various views of the bitegmic, basitropic and campylotropous ovules. A. Section showing the central carpellary hole as the septal arms with septal axials (SA) are established. B. Section above A showing the freed gynoecium with a carpellary hole and lacking septal axials. Septal arms subdivision occurs along the IT radii (arrows). C. Overview section above B showing freed floral parts and the central carpellary hole. D. Section above C showing the subdivided septal arms with ventrals (V) near the inner appressed septal wing tips. E. Young floral bud section showing floral epigyny around a separating gynoecium (arrows), compare with A and E. F. Section above E showing a freed, immature gynoecium surrounded by fused stamens and tepals. Protandry is evident when compared to C.

stylar or stylodial area of the capsule (Fig. 2E) and continues along the zone where the septal arm tips meet (Fig. 7D).

In most liliaceous species with a superior ovary, tepals, stamens and their vasculatures are well established below the level at which locules open and ovules are supplied. However, this is not the case in *S. occidentale* and other members of the Veratreae due to an inferior gynoecium and varying degrees of perianth

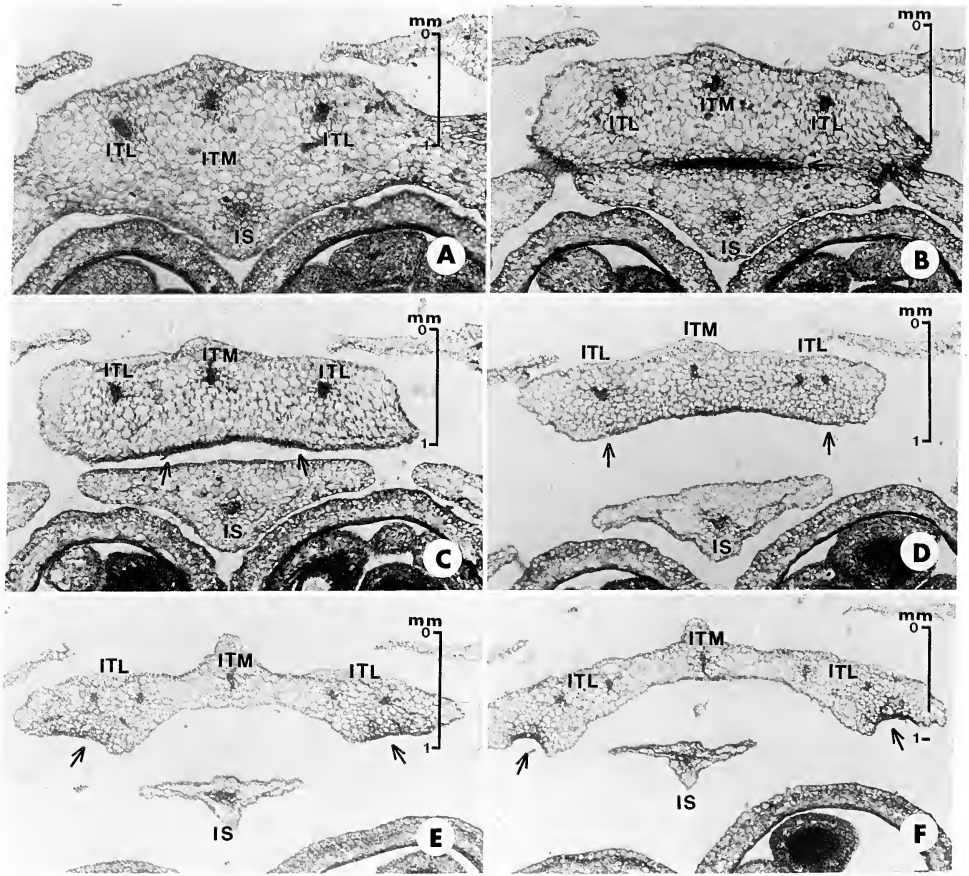


Fig. 8.—Series of transverse sections from an inner tepal of *S. occidentale* showing tepal vascularization and the v-shaped adaxial nectary. (The outer tepal nectary and vascularization is similar.) A. Transverse section showing inner tepal and stamen epitepaly and lateral fusion to outer tepals (arrows), compare to Fig. 7E, F. An inner tepal median (ITM), two inner tepal laterals (ITL) and an inner stamen (IS) bundle are shown. B. Origin of nectiferous zone between inner tepal and stamen (arrow). C. Inner tepal freed from the dilated inner stamen, arrows indicated adaxial nectiferous zone. D. Increased width of nectiferous zone (arrows) with division of two ITL shown. E. Lateral localization of nectiferous surface into a v-shape is associated with enlarged margins and an abaxial mid-rib and four ITLs. F. Further lateral localization of nectiferous surface along the adaxial tepal margins (arrows).

fusion. In *S. occidentale*, formation of tepal and stamen vasculatures occurs above the level at which the ovules are supplied (Fig. 6, 7A, B). The insertion and departure of the tepals and stamens follow a spiral pattern in forming an imbricated floral tube. Throughout much of the narrowly campanulate flower, the freed outer tepals overlap the inner (Fig. 7C, 7E, F, 8, 9). The pale greenish yellow to purplish brown nodding flowers have narrowly lanceolate tepals with spreading, recurved, acuminate tips (Fig. 2A–C, 4). Basally above the epigynous zone the tepals are connate for a short distance. Epitepaly occurs among both the outer and inner stamens. A bilobed or v-shaped nectiferous zone occurs adaxially on the freed tepals. The stamens, which average 7.0–8.5 mm long, are included. The anthers are located at the level at which the tepal tips recurve. The gynoecium and styles



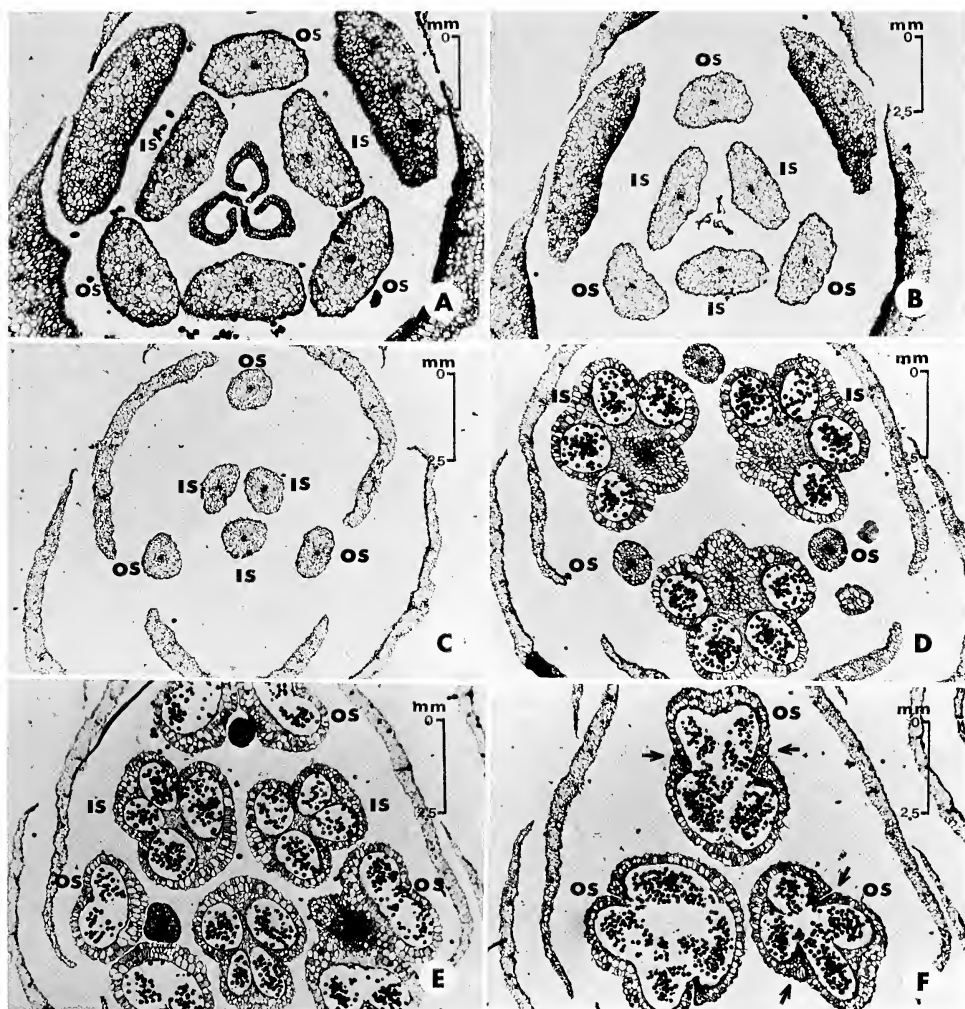
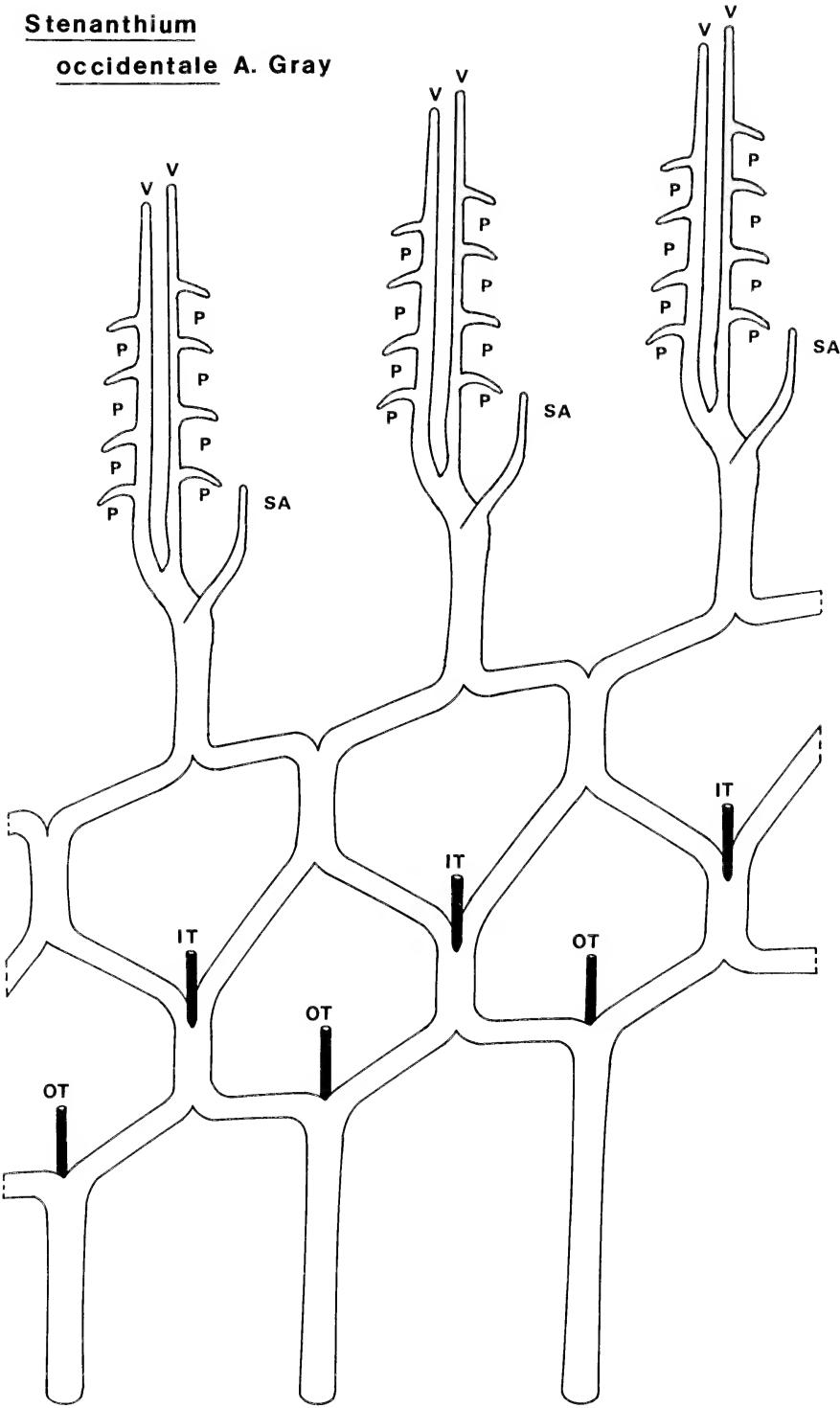


Fig. 9.—Stamen vascularization and dimorphic filament morphology of a young bud of *S. occidentale*. A. Transverse section above the epitepaly zone showing six basally dilated filaments. Adaxial nectiferous zones on both the outer and inner tepals are evident as well as three open styles. B. Transverse section above A showing three inner filaments (IS) surrounding three freed styles adaxially and three outer filaments (OS) abaxially. C. Section above B showing the central inner filaments (IS) and divergent outer filaments (OS). D. Section above C showing adaxial inner anther attachment as the outer filaments (OS) remain peripherally. The four apparent thecae are confluent terminally. E. Section above D showing adaxial attachment of outer anthers and the centrally located inner anthers. F. Section above E showing the upper confluent thecae of the three outer anthers (OS), arrows indicate dehiscence zones.

are much shorter than the stamens when the anthers dehisce. However, the mature fruiting gynoecium far surpasses the withered, persistent perianth (Fig. 2D) and the degree of observable inferiority is greatly reduced (Fig. 11).

Six complex, compound bundles established in the lower receptacle levels are ultimately responsible for the complete tepal and stamen vascularization. These compound bundles have been designated the compound OT bundles (dorsal-

**Stenanthium**  
**occidentale** A. Gray



compound bundle; Sterling, 1982) and the compound IT bundles (“zwischen-bundel”; Sterling, 1982), respectively, for they are positioned along those respective radii. A description of the resulting vascularization from one compound OT and IT bundle will illustrate the patterns for both sets of tepals and stamens since the six bundles involved are all free from each other (Fig. 10).

In the upper epigynous zone, a compound OT bundle appears triangular in cross-section (Fig. 5B–F, 6A, C, E, F). Several complex subdivisions occur within the compound OT bundles which results in the formation of an outer tepal median (OTM), two outer tepal laterals (OTL), an outer stamen bundle (OS) and a dorsal (D). The OTM is established first and after its departure, the remaining product undergoes a rapid subdivision in which two laterals (OTL), outer stamen (OS) and dorsal (D) bundles are established. The OTM, OS and D bundles all lie along the same radius with normally arranged xylem (adaxial) and phloem (abaxial) (Fig. 5C). It should be noted that the outer tepal laterals (OTL) are derived from the remaining product bundle, not the outer tepal median (OTM). Each outer tepal receives three bundles or traces, an outer median (OTM) and two laterals (OTL). The laterals undergo further radial divisions to establish additional laterals. In a freed, mature outer tepal, a seven, rarely more, bundled condition is typical, that is three outer tepal laterals (OTL) + outer tepal median (OTM) + three outer tepal laterals (OTL).

The origin of the inner tepal median (ITM), the two inner tepal laterals (ITL), and an inner stamen bundle (IS) from a common IT bundle is similar to that of the outer series vascularization (Fig. 5B–F, 6A, C, E, F, 7A–D). The ITM, two ITLs and IS bundles all have normally arranged conducting elements. The only difference in outer and inner vascularization which arose from compound OT and IT bundles, respectively, is that a dorsal (D) is associated with subdivision of the compound OT parental bundle, and there is no counterpart with the compound IT bundle.

Each inner tepal is supplied with three bundles or traces, an inner median (ITM) and two laterals (ITL). The laterals undergo further radial divisions, as in the outer cycle, to establish a seven bundled condition (Fig. 7C, E, F, 8). A freed, mature inner tepal has three inner tepal laterals (ITL) + inner tepal median (ITM) + three inner tepal laterals (ITL). There is no fusion between any of the laterals or between laterals and medians in either set of tepals. Each bundle or traces follows a parallel course and ends near the laminal tepal margins.

The outer filaments are ca. 0.75–1.5 mm longer than the inner filaments (Fig. 9). The dimorphic filaments present a greater vertical zone of pollen dispersal within the imbricated tepals, than if the filaments were the same length. The extrorse anthers which are basifixed have a valvular dehiscence between the confluent thecae that opens into a reniform, peltate disc (Fig. 9). The endothecium

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Fig. 10.—Roll-out longitudinal summary diagram for the floral vasculature of *S. occidentale*. A spiral pattern is indicated in the formation and departure of the various letter coded and text discussed bundles: OT = compound outer tepal, IT = compound inner tepal, V = ventral, P = placental and SA = septal axial. The following bundles which are not shown result from the subdivision of the following two bundles, respectively: from the compound OT bundle results the OS (outer stamen), OTM (outer tepal median), OTL (outer tepal laterals) and D (dorsal), and from the compound IT bundle results the IS (inner stamen), ITM (inner tepal median) and ITL (inner tepal laterals).

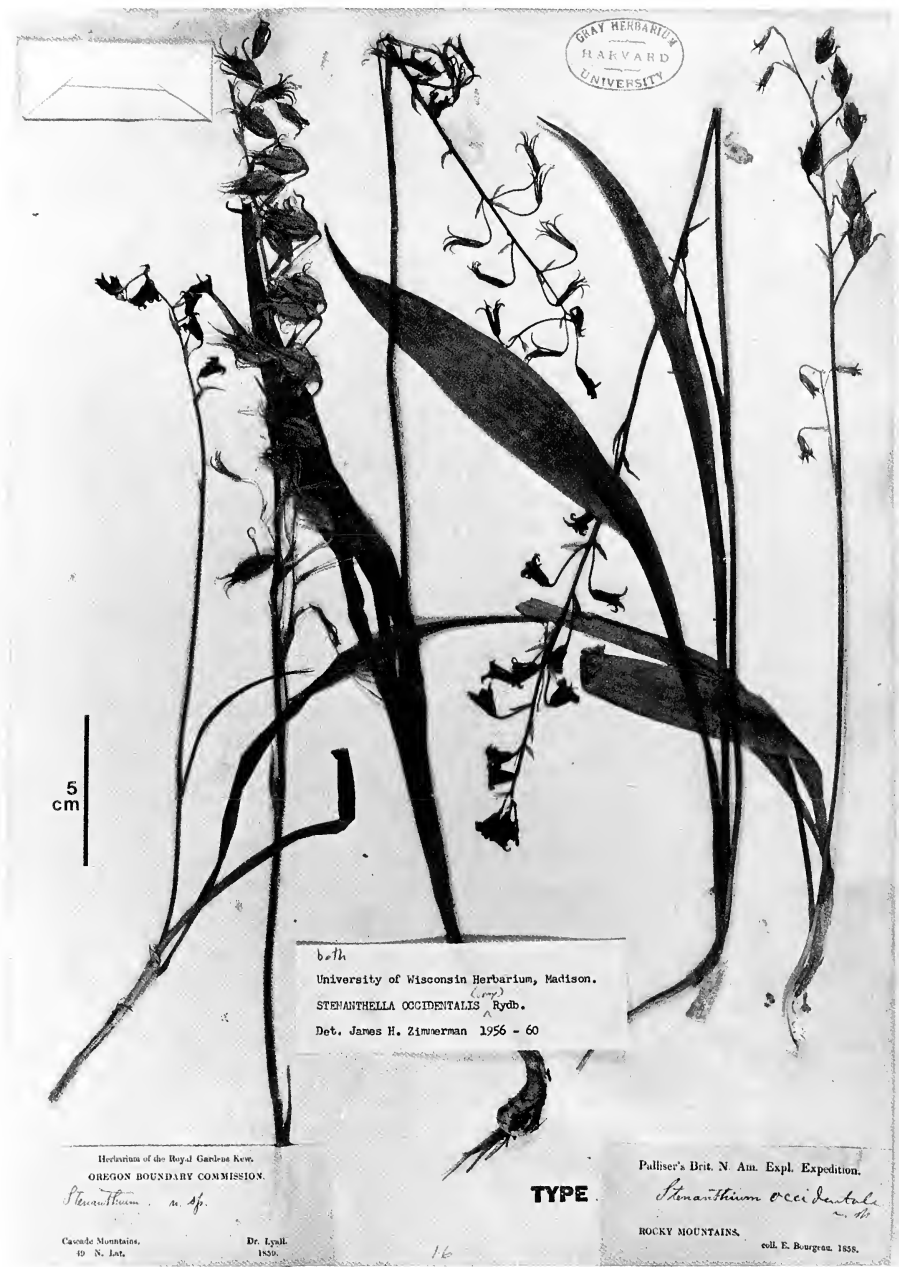


Fig. 11.—Lectotype (right element) and paratype (left element) of *S. occidentalis*. (Courtesy of Gray Herbarium, Harvard University)

has wall thickenings or bands of the girdle type (Dahlgren and Clifford, 1982). Protandry occurs within each flower of *S. occidentalis*, since both outer and inner anthers dehisce at the same time, and this is earlier than gynoecial maturity (Fig. 7C, E, F, 9).

### Geography and Taxonomy

*Stenanthium occidentale* occurs in British Columbia from 52°N Latitude southward into the Rocky Mountain Trench to northern Idaho and Montana as well as southward at higher elevations in the Cascade and Coast Ranges of western Washington, western Oregon and northwestern California (Fig. 1). The species occurs between 3800–6500 ft in Del Norte, Humboldt, Siskiyou and Trinity counties, California (Jepson, 1921, 1923; Munz, 1973; Ferlatte, 1974), but near sea level on Vancouver Island, the Olympic Peninsula and the Columbia River Gorge. Neither specimens nor reports are known from Alaska (Anderson, 1945; Hultén, 1968), Wyoming (Dorn, 1977) and Queen Charlotte Island, British Columbia (Carter and Newcombe, 1921; Taylor, 1966; Calder and Taylor, 1968). Frequent in coniferous to subalpine zones, this species occurs on wet cliffs, mossy stream banks, rocky crevices, moist montane thickets, and meadows. In northern areas, it is commonly an understory associate of *Abies*, *Thuja*, *Tsuga* and *Pseudotsuga*.

In describing *S. occidentale*, Asa Gray (1873) listed a syntypic series of five collections: Rocky Mountains, 1858, Bourgeau; Cascade Mountains, 49°N Latitude, 1859, Lyall; Kootenay, 1860, Lyall; Rocky Mountains, 49°N Latitude, 6000 ft, 1861, Lyall; and foothills of Cascade Mountains, mossy banks of stream, 1871, Hall. Baker's review (1879) cited only Bourgeau, Lyall and Hall collections without selecting a type. Rydberg (1900), in transferring *S. occidentale* and *S. sachalinense* to *Stenanthella* on the basis of a superior ovary, cited numerous specimens for *Stenanthium occidentale*, but only Bourgeau's collection was included from Gray's syntypic series. Piper (1906), Jepson (1921), and Hitchcock et al. (1969) in their typification stated "Bourgeau, Rocky Mountains." Since the Bourgeau specimen at the Gray Herbarium (Fig. 11) is stamped "type" and was mentioned first by Gray (1873) in his syntypic series, it should be designated the lectotype.

### *Stenanthium occidentale* A. Gray, 1873

*Stenanthium occidentale* A. Gray, Proc. Amer. Acad., 8:405. 1873.

**Lectotype.**—Rocky Mountains, Palliser's British North American Exploratory Expedition, *E. Bourgeau s.n.*, 1858 (GH!, here designated; photo CM)—Fig. 11.

**Isolectotypes.**—(B, K, NY!; photo CM).

**Paratypes.**—Oregon Boundary Commission, Cascade Mountains, 49°N Lat., 1859, *Lyall s.n.* (GH!, photo CM; Fig. 11); Oregon Boundary Commission, Cascade Mountains to Fort Colville, about 49°N Lat., Cascade Mountains, July 1860, *Lyall s.n.* (GH!, photo CM); Oregon Boundary Commission, from Fort Colville to Rocky Mountains, Rocky Mountains, Lat. 49°N at 6000 ft above sea level, 1861, *Lyall s.n.* (GH!, photo CM); Oregon, foothills of the Cascade Mountains, mossy banks of stream, 1871, *E. Hall 535* (F!, GH!, MO!-2 sheets, NY!-3 sheets; photos CM).

*Stenanthella occidentalis* (A. Gray) Rydberg, Bull. Torrey Bot. Club, 27:531. 1900.

*Stenanthium rhombipetalum* Suksdorf, Werdenda, 1:6. 1923.

**Lectotype.**—Washington, Skamania County, Cape Horn along Columbia, 27 May, 29 June 1920, *W. Suksdorf 10,466* (GH!, photo CM).

**Isolectotypes.**—(DS!, MO!, NY!-2 sheets, UC!, WTU!; photos CM).

**Representative specimens examined.**—CANADA: ALBERTA: Near Banff, *Scott s.n.* (DAO), *Canby s.n.* (GH, US); Banff, *Olson s.n.* (GH), *Rusby s.n.* (NY), *Phillips s.n.* (CM), 4550 ft, *Hermann 12657* (US); Baker Creek, *Kojima s.n.* (DAO); Waterton Lakes, *Macoun 13850* (GH), *Moss 1003* (DAO); Crypt Lake, 6400 ft, *Senn 2639* (DAO); Red Rock Canyon, 4500 ft, *Breitung 16098* (F, NY), 5000 ft, *de Vries 2127* (DAO); Red Rock Nature Trail, *Sudol 115* (DAO); Moraine Lake, *Hallis 5727* (MO), *McCabe 5227* (UC); Bertha Lake, 4200–4600 ft, *Malte & Watson 282* (GH), 4400 ft, *Hermann 13064* (US); Devil's Lake, *Sanson 22126* (CM); Alderson Lake, *Moss 510* (DAO, GH); Summit Lake, 5500 ft, *Moss 547* (GH); Headwaters of Saskatchewan & Athabasca Rivers, S of Summit, *Brown 1547* (GH);

Rowe Lake, *Scotter 10014* (DAO); Sulphur Mt., *van Brunt 97* (NY), *Sanson s.n.* (DAO), *Jenkins 1424* (DAO), 5000 ft, *McCalla 2217* (NY, US); Crow Nest Pass, *Macoun 25101* (NY); Ptarmigan Valley to Pipestone Valley, 6000 ft, *Brown 432* (GH, MO, NY); Lake Louise, *Olson s.n.* (GH), *Jones s.n.* (WTU), *Fraser 4* (DAO), *Dempster 1237* (JEPS), Big Beehive, *Beattie 5249* (DAO); Valley of Ten Peaks, *MacCallum s.n.* (CAS); Spray River, *Degener 2409* (NY); Tunnel Mt., *Malte & Watson 835* (GH); Marble Canyon, *Turner s.n.* (DAO), *Groh s.n.* (DAO); Sundance Canyon, *McCalla 4555* (DAO); Sundance Camp, *McCalla 4555* (GH); Johnson Canyon, 1500–1700 m, *Boivin 4741* (DAO); Johnston Creek, Hillsdale, *Mair 153* (UBC); Cascade River, Lake Minnewanka, *Jenkins 1600* (DAO); N of Coleman, W flank Livingstone Range, *Norris 81* (DAO); Livingstone Falls, 5900 ft, *Hermann 12766* (US); Sugarloaf Mt., NW of Livingstone Gap, 7700 ft, *Dore et al. 20524* (DAO); Morley, *Packer s.n.* (DAO); Eisenhower Junction, Vermilion Pass, 5500 ft, *Ogilvie s.n.* (UBC); Between Dolomite & Cirque Peaks, *Calder & MacKay 32752* (DAO); Larch Valley, 7200 ft, *Vrugtman s.n.* (DAO); Consolation Valley, 6200 ft, *Beamish & Vrugtman 620159* (DAO, UBC); Pigeon Creek, 5500 ft, *Whitehorn 504* (DAO); SW of Exshaw, NW of Pigeon Mt., *Brunton 1137* (DAO).

**BRITISH COLUMBIA:** Rocky Mts., 5000 ft, *Macoun s.n.* (MO); Rocky Mts. & Pacific Coast, *Freeman s.n.* (GH); Selkirk & Rocky Mts., 7500 ft, *Shaw 338* (CM, GH, MO, NY), 7000 ft, *Macoun 338* (US); Skagit Valley, 5000 ft, *Macoun 70219* (CM); Chilliwack Valley, *Macoun 54078* (GH, NY, US); Bow River Pass, *Macoun s.n.* (GH, NY); Emerald Lake, 4300 ft, *Macoun 118* (NY), 4200 ft, *Brown 332* (GH, MO), *Marquand 53* (NY); Bella Coola, Clayton Falls, *Leamon 145* (UBC); Lastsqaw Creek, *McCabe 1476* (UC); Natural Bridge, 4000 ft, *Ulke 6* (CAS); Little Yoho Valley, *Bostock s.n.* (DAO), *Comte 1721* (MO); Yoho Valley, *Eastham s.n.* (UBC), *Fleming s.n.* (UBC); Point Lace Falls, *Lane s.n.* (CM), *McCalla 7144* (UBC); Takakkaw Falls, 4900 ft, *Calder & Saville 12020* (DAO); Yoho Pass, *Walcott s.n.* (US), Vermilion Pass, *McCabe 5180* (UC); Kicking Horse Lake, *Macoun s.n.* (GH, US, NY); Glacier, *McCallum s.n.* (CAS), *Doane s.n.* (DS); Mt. Cheam, *Fletcher 1872* (DAO); Spuzzum Creek on Hope-Lytton highway, *Calder & Saville 8411* (DAO, UBC); Penticton, Green Mt. Road, *Stonor s.n.* (UBC); Mt. Brent, W of Penticton, 5500 ft, *Calder et al. 2057* (DAO), 5000 ft, *Eastham s.n.* (UBC); SW of Penticton, 6800 ft, *Calder & Saville 12269* (DAO, NY), 6000 ft, *Krause 681951* (UBC); Hope-Princeton area, 5000–6500 ft, *Fedor s.n.* (UBC); Hope, *Eastham s.n.* (DAO, UBC); Tulameen River, *Kemp s.n.* (NY); Manning Park, W on Hope-Princeton highway, 4300 ft, *Calder & Saville 11562* (DAO), *Krajina s.n.* (UBC), Orchid Meadow, 3700 ft, *Beamish et al. 9084* (GH, UBC), Ellis Peak turn-off, 6500 ft, *McLean s.n.* (DAO), Paddy Lake road, 6000 ft, *McLean s.n.* (DAO); Mt. Apex, E of Nickel Plate Mine, 5600 ft, *Calder & Saville 10741* (CAS); Hedley, Nickel Plate Mine, *Vrugtman 5* (UBC), McNulty Creek road, 4000 ft, *Grant s.n.* (DAO); Nickel Plate townsite, SE of Hedley, 5700 ft, *Beke & Marchand s.n.* (DAO); Goodchap Mt., 5000–7000 ft, *Martin s.n.* (UBC); Apex Alpine Ski area, *Spellenberg & Soreng 5633* (NY); Ashnola District, Cathedral Lakes, 7000 ft, *Taylor 1311* (UBC, UC); Cathedral Park, Ewart Creek Valley, 1200 m, *Hainault 7598* (DAO), *Hainault 7902* (DAO); Noisy Creek, Ashnola Forks, 5000 ft, *Barr 9320* (UBC); Ashnola Range, 49°07'N, 120°08'W, 5600 ft, *Calder et al. 19559* (DAO, UC, WTU); SW of Okanagan Falls, 3800 ft, *Calder & Saville 9933* (DAO, UC, GH); Nelson, Six Mile Lakes, *Eastham s.n.* (UBC), Silver King Mine, 5000–6000 ft, *Eastham s.n.* (UBC); NNE of Nelson, Duhamel Creek, 3100–3300 ft, *Calder & Saville 9389* (DAO); SW of Nelson, Copper Mt., 7000 ft, *Calder & Saville 12271* (DAO); Kootenay, Floc Lake, 4000 ft, *Hume 704* (UBC); Kootenay, Sinclair Nature Trail, 3475 ft, *Seel 39* (DAO); Stanley Peak Valley, 51°11'N, 116°05'W, *Calder & MacKay 32795* (DAO); Moyie, between Creston & Cranbrook, 3100 ft, *Calder & Saville 9235* (DAO, NY, UC, WTU); Mouse Creek, Fort Steele, *Fodor 53* (UBC); Fernie, Coal Creek, *Eastham s.n.* (DAO, UBC); Estelle Mine, Wasa, 5000 ft, *Grant s.n.* (DAO); N of Bull River, 49°37'N, 115°25'W, 5200 ft, *Taylor & Ferguson 2717* (DAO); Elk River Valley, 20 mi N of Natal, *Weber 2257* (GH); Starvation Peak area, 49°02'N, 114°12'W, 6300 ft, *Taylor et al. 3412* (DAO); Flathead, 4000 ft, *Bell & Davidson 42* (DAO); SE of Flathead townsite, Flathead River, 5200 ft, *Taylor & Ferguson 2057* (DAO); Flathead Summit, *McCabe 4997* (UC); Mt. Stephen, *Fogg s.n.* (UBC); NE of Canal Flats, N of junction of Albert & Ralliser Rivers, 3900 ft, *Taylor & Ferguson 1488* (DAO); Fairmont Hot Springs, Flat Creek, *Eastham s.n.* (UBC); W of Windermere, Paradise Mine, Toby Creek, 5200 ft, *Calder & Saville 11346* (DAO); Paradise Mine, Invermere, *Hardy s.n.* (DAO); Radium Hot Springs, *Eastham s.n.* (UBC), *Calder & Saville 11177* (DAO); NW of Takakkaw Falls, 6000 ft, *Hitchcock & Martin 7700* (DS, GH, MO, NY, UC, WTU); Othello, Mt. Ogilvie, 3500 ft, *Brayshaw s.n.* (UBC); Mt. Copley, 3000–3500 ft, *Beamish 232* (UBC); Mt. Assiniboine, Sunburst Lake, 7200 ft, *Scamman 6600* (GH); Frosty Mt., 4400 ft, *Calder et al. 15673* (GH); Canim Mine, *Beamish & Stone 7574* (UBC); NE of Pollock, 49°22'N, 114°34'W, 6500 ft, *Taylor & Ferguson 2916* (DAO); Upper Sage Creek Valley, 5200 ft, *Beamish et al. 747* (UBC); San Joseph Bay, 20 ft, *Anderson & Dejardin 9* (UBC); Moss Lake, *Pajar & Pinder-Moss 64* (UBC). VANCOUVER ISLAND, *Macoun s.n.* (GH), 5000 ft, *Calder & MacKay 32586* (NCU); Port Alice, 2200 ft, *McComb & Watson s.n.* (UBC); Kyuquot, 100 m, *Taylor & Szczawinski 359* (UBC); Power River, 50°12'N, 127°30'W, 560



m, *Jones s.n.* (DAO); Crest Creek along Gold River road, *Calder & MacKay 31786* (DAO); Great Central Lake, *Buckland s.n.* (UBC); Forbidden Plateau, *Cumming s.n.* (UBC); Mt. Becher, 2900 ft, *Calder & MacKay 31906* (DAO); Mt. Arrowsmith, *Carter s.n.* (GH, US), *Baker 938* (CAS), *Howell 7619* (CAS), 3500 ft, *Jeffery s.n.* (UBC), 3400 ft, *Schmidt s.n.* (DAO); Markale, *Taylor & Szczawinski 211* (UBC); Cameron Lake, *McBey s.n.* (UBC), 2500 ft, *Eastham s.n.* (UBC); Port Alberni, *Calder et al. 19427* (DAO); Home Lake, *Macoun s.n.* (MO); Port Alberni-Sarita road, N of Franklin River, *Calder & MacKay 30329* (DAO); Alberni, *Carter s.n.* (GH); Mt. Joan, Beaufort Range, 2500–3000 ft, *Calder & MacKay 32334* (DAO); Deep Lake, 3500 ft, *Schmidt s.n.* (DAO); Between Kennedy & Taylor Rivers on Port Alberni-Tofino road, *Calder & MacKay 30661* (DAO); Sprout Lake, *Meyer 1543* (GH, MO, NY, UC, US), *Taylor 1252* (UBC), *Calder & MacKay 30682* (CAS); Fourth Nanaimo Lake, 300 m, *Krajina et al. 4741* (UBC); Nanaimo River Valley, 930 ft, *Mueller-Dombois 101-1* (UBC), 300 m, *Krajina et al. 5126* (UBC); Englishman's River, 3300 ft, *Schmidt s.n.* (DAO); Estelle, 300 m, *Krajina et al. 4801* (NY, UBC); Moat Lake, 4000 ft, *Underhill s.n.* (UBC, WTU), *Calder & MacKay 32280* (DAO); Elk River Falls, W of Campbell River, *Calder & MacKay 30416* (DAO); Elk River, 1000 ft, *Young & Hubbard 579* (DAO); Elk Pass, 50°34'N, 115°04'W, 6200 ft, *Taylor & Ferguson 3611* (DAO); Junction Upper Campbell Lake & Battle Lake, *Calder & MacKay 30583* (DAO, NCU); Gail Falls on Kelsy Bay-Campbell River road, 50°16'N, 125°49'W, *Calder & MacKay 32439* (DAO); Burman Lake, 4400 ft, *Calder & MacKay 32491* (DAO, UBC, UC), 5000–6000 ft, *Krajina et al. 68081* (UBC); Below Mt. Burman, 5000 ft, *Calder & MacKay 32586* (DAO); Kennedy River, 450 ft, *Young & Hubbard 285* (DAO); Kennedy Lake, *Wade et al. 200* (UBC), 200 ft, *Pajar 144* (UBC); Cowichan Lake, *Rosendahl 1805* (GH, MO, NY, UC), *Spilsbury s.n.* (DAO).

**UNITED STATES: CALIFORNIA:** DEL NORTE Co.: Siskiyou Mts., *Brandegee s.n.* (GH); Waldo to Black Butte, *Eastwood 2150* (CAS); S Fork Smith River, 300 ft, *Adams s.n.* (HSC); Preston Peak, Bear Basin, Gasquet, 4701 ft, *Clifton & Griswold 5732* (HSC). HUMBOLDT Co.: Trinity Summit Range, Happy Camp Mt., 4200 ft, *Tracy 15558* (DS, GH, JEPS), 4200 ft, *Tracy 18172* (UC), 4200 ft, *Tracy 18517* (UC), Box Camp, 4800 ft, *Tracy 17901* (UC); Near Tish Tang A Tang Creek, S Fork, Hoopa, 4649 ft, *Gilbert & Muth 11524* (HSC); Salmon Mts., Mill Creek, Middle Fork, Hoopa, 4400 ft, *Overton 12360* (HSC), 5551 ft, *Clifton & Griswold 11935* (HSC); Whiteys Peak, 4998 ft, *Kearns 434* (HSC). SISKIYOU Co.: Preston Peak, Rattlesnake Meadow, 5400 ft, *Montalvo & Ackerman 425* (HSC), 5000 ft, *van Deventer s.n.* (HSC); White Mt., T 47N, R 10W, S 10, *Wheeler 3181* (CAS, GH); Canyon Creek, 6300 ft, *Tucker et al. 3747* (CAS, UC); Paradise Lake, 6300 ft, *Alexander & Kellogg 5857* (DS, UC, WTU); Hammond, Kelsey Creek, 5000 ft, *Hoffman 4043* (UC); Marble Gap Trail, 6000 ft, *Muth 427* (CAS); Marble Mts., Spirit Lake, 6000 ft, *Howell 15070* (CAS); Marble Valley Guard Station, *Stillman 364* (HSC); Klamath National Forest, Siskiyou Mts., Cook & Green Pass, 3500 ft, *Smith 9962* (HSC), 4000 ft, *Roderick 6487* (UC), *Roderick 65106* (JEPS); Black Mt., *Muth s.n.* (CAS); Black Marble Mt., Pacific Crest Trail, *Sawyer & Mesler 4050* (HSC). TRINITY Co.: Trinity Alps Wilderness Area, Union Creek, 6100 ft, *Hall 8626* (UC), 5700 ft, *Goforth 280* (HSC); Sapphire Lake, 6100 ft, *Sawyer 2359* (HSC).

**IDAHO:** ADAMS Co.: S side Ruth Lake, ca. 16 mi SSW of Riggins, T 22N, R 2W, S 15, 7250 ft, *Bingham & Miller 446* (ID). BONNER Co.: Hope, *Leiberg s.n.* (MO, ORE); Green Monarch Mt., *Dunkle s.n.* (ID); Pack River, Colburn, 2100 ft, *Ripley & Barneby 10940* (CAS). BOUNDARY Co.: Snowy Top, *Christ 5995* (ID, NY); Port Hill, Smith Creek, 4500 ft, *Roszbach 273* (DS, WTU); Smith Peak, 6000 ft, *Roszbach 274* (DS); N Fork Hunt Creek, *Daubenmire 44372* (NY, WTU); Three Ponds area, T 61N, R 2W, S 11, 3400 ft, *Wellner 2659* (ID); Upper Priest River Valley, Upper Priest Falls, 2900 ft, *Henderson & Cholewa 6789* (ID). CLEARWATER Co.: N Fork Clearwater River, junction main fork, *Sharsmith 3574* (GH, UC, WTU); Clearwater National Forest, Aquarius, 1670 ft, *Wellner 1755* (ID). IDAHO Co.: Headwaters of Squaw Creek, 5400 ft, *St. John & Muller 8389* (UC); Lowell, Three Devils Creek, Middle Fork Clearwater River, *Constance et al. 1084* (MO, UC); Lowell, Three Devils Camp, *Meyer 916* (GH, MO), *Davis 3443* (CAS), *Baker 14805* (ID, NY); Selway River, SW of Lowell, *Christ 12094* (ID), *Christ & Ward 12094* (NY); Falls of Selway River, *Thompson 1668* (WTU), *McMullen 1517* (ID); Meadow Creek, *Gail s.n.* (ID), *Botany 54 Class* (ID); Seven Devils Mt., Brundage Trail at head of Sheep Creek, 6600 ft, *Packard 454* (UC), *Christ 12698* (NY); Hells Canyon Recreation Area, 11 mi WSW of Riggins, T 23N, R 2W, S 12, 7100 ft, *Bingham & Miller 407* (ID); W of Riggins, *Baker 11999* (ID, NY). KOOTENAI Co.: *Leiberg s.n.* (F, NY); Watson Woods, *Leiberg 125* (WTU). SHOSHONE Co.: Coeur d'Alene Mts., Stevens Peak, E of Wallace, 1750 ft, *Leiberg 1479* (GH, MO, NY, ORE); Priest Lake, *Piper 3691* (GH); Creek Pass, *Baker 16939* (WTU); Upper Priest River, 3000 ft, *Epling 7071* (MO); St. Joe River Canyon, Avery, 3300 ft, *Henderson & Cholewa 6653* (CM).

**MONTANA:** FLATHEAD Co.: Columbia Falls, Flathead River, Bad Rock Canyon, *Rogers 995* (MO, NY, WTU); Loneman Mt., 4400 ft, *Parke 15* (UC); Whitefish, *Stickney 1228* (GH). GLACIER Co.: Glacier National Park, *Russell s.n.* (GH), *van Dyke s.n.* (CAS), *Phelps s.n.* (CM); Mineral Park, *Jones s.n.* (DS); Iceberg Lake, *Young s.n.* (TEX); Logan Pass, *Schreiber 1333* (UC), *Henry s.n.* (CM); Kootenai

Lake to Waterton Ranger Station, *Harvey & Marshall* 4283 (MO, NCU); Canyon Creek, 5800 ft, *Brant* 66 (WTU). LINCOLN Co.: Cabinet Mts. Wilderness Area, Leigh Lake, 6500 ft, *Woodland* 694 (DS), *Thomas* 12280 (DS). MISSOULA Co.: Ridge between Hillgate & Big Blackfoot Rivers, *Watson* 428 (GH); Big Blackfoot River, *Canby* 332 (NY); Woodruffs Falls, Upper Meanas Pass, *Canby* 332 (GH); Headwaters of E Fork Flathead River, *Canby* 332 (NY); Columbia Falls, *Williams* 917 (US), *Williams s.n.* (NY); Glacier National Park, *Hitchcock* 11938 (US), 1650–1950 m, *Standley* 16705 (US); Sperry Glacier, *Umbach* 18553 (WIS); Blackfoot Glacier, *Jones s.n.* (DS, MO); Gunsight Pass, *Dunkle s.n.* (ID); Gunsight Lake, *Maguire* 644 (UC); Lake Josephine, *Standley* 15236 (US); Lake McDermott, *Standley* 15911 (US); Lake McDonald, *Umbach* 363 (WIS, MO); Little St. Mary's Lakes, *Umbach* 821 (WIS, MO); Grinnell Lake, *Hollis* 5728 (MO); Cracker Lake Trail, *McLaughlin* 763 (MO); Granite Park Chalets, *Standley* 16256 (US); Dawson Pass, *Somes* 51 (NY); Woodman, 4500 ft, *Kirkwood* 1477 (GH, UC); Copper Cliff, 5000 ft, *Hitchcock* 1826 (CM, DS, GH); Midvale, *Umbach* 247 (DS, MO, NY, US).

OREGON: Willamette Slough, *Howell s.n.* (GH); Cliffs along Columbia River, Cascades, *Howell s.n.* (ORE); Columbia River, *Howell* 894 (CAS, US); Cascades, *Howell* 579 (CM); *Parry* 1016 (US). CLACKAMAS Co.: Eagle Creek, *Henderson s.n.* (ORE, OSC); Clackamas River, S of Rhododendron Creek, 2400 ft, *Wright* 1710 (OSC). CLATSOP Co.: Astoria, *Anderson s.n.* (DS, GH); Saddle Mt., 2900 ft, *Patterson* 45 (ORE), *Ifft* 15 (DS; OSC), *Rosbach* 392 (DS, WTU), *Gilkey s.n.* (OSC, WTU), 3250 ft, *Detling* 6456 (DS, ORE, UC), *Dennis* 2545 (DAO, DS, US), 2650 ft, *Dennis* 2592 (OSC); W peak of Saddle Mt., *Howell* 28443 (DAO); Onion Peak, 3064 ft, *Chambers* 3227 (NY, OSC); Sugarloaf Mt., SE of Cannon Beach, 2800 ft, *Chambers* 3789 (OSC, WTU). CURRY Co.: Onion Camp, 4500 ft, *Leach* 2960 (ORE, OSC); Siskiyou National Forest, Kalmiopsis Wilderness Area, 3760–4160 ft, *Denton* 2341 (ID, NY, WTU). HOOD RIVER Co.: Mt. Hood National Forest, Lost Lake, *Gooding & Evinger* 45 (OSC), *Peck* 9914 (WILLU), *Henderson* 800 (MO); Dry Creek Falls, Cascade Falls, *Gustafson* 151 (OSC); Columbia Gorge, W of Wyeth, 100 ft, *Detling* 7253 (DS, ORE). JACKSON Co.: Siskiyou Mts., Whisky Peak, Star Ranger Station, 4000 ft, *Robbins* 3588 (JEPS). JOSEPHINE Co.: *Howell s.n.* (ORE); S of Takilma, *Peck* 8024 (WILLU); E Fork Illinois River, *Peck* 8024 (GH); W Fork Williams Creek, Cave Camp, *Applegate* 5102 (DS), *Applegate* 8725 (DS), Cave Trail, *Applegate* 5116 (DS); Grayback, Layton ditch, *Savage s.n.* (ORE); Grayback Mt., Williams Creek, *Henderson* 12826 (ORE); Peavine Lookout, 3000 ft, *Priebe s.n.* (OSC); Oregon Caves National Monument, No Name Creek, *Baker & Ruhle* 450 (ID, NY); W of Selma, Store Gulch, *Steward s.n.* (OSC). LANE Co.: Belknap Springs, *Peck* 2616 (WILLU); Dorena, Bohemia, Sharp Creek, *Constance s.n.* (UC); E Fork McKenzie River, T 16S, R 5E, S 5, 1400 ft, *Detling* 2849 (ORE); Big Fall Creek, Hette Camp, *Henderson* 18729 (ORE); S of Oakridge, *Peck* 22072 (UC); Lookout Creek Basin, T 15S, R 6E, S 30, 3000 ft, *Franklin & Dyrness* 167 (OSC); Willamette National Forest, Walker Creek Trail, Lowder Mt., *Utech* 78–275 (CM). MARION Co.: N Silver Creek, below Falls, *Foster s.n.* (ORE); Detroit, Santiam River, *Peck* 1667 (WILLU); Silver Creek Falls, *Nelson* 2240 (GH). MULTNOMAH Co.: Sandy River, *Henderson s.n.* (ORE, OSC); Columbia River, Multnomah Falls, *Howell s.n.* (MO), *Peck* 1386 (WILLU), *Peck* 2035 (GH), *Piper* 6267 (GH, US), *Thompson* 2703 (DS, WILLU); Bridal Veil, *Jackson s.n.* (OSC); Latourelle Falls, *Thompson* 4350 (DS, MO, WTU); Wakenah, *Leach* 1325 (ORE); McCord Creek, Warrendale, *Jaques s.n.* (OSC), 3000 ft, *Thompson* 11872 (DS, MO, NY, WTU); Oneonta Gorge Trail, 65 ft, *Ireland* 3242 (ORE); Wahkeena Falls, *Buddenhagen* 5 (OSC); Crown Point, 210 ft, *Bacigalupi et al.* 7885 (JEPS). TILLAMOOK Co.: Cascade Mts., *Kellogg & Harford* 1025 (GH); Columbia River, *Howell* 374 (CAS, CM, NY), *Eggert s.n.* (MO), *Parry* 1016 (US), *Dickson* 4853 (NY), *Dickson* 8432 (MO); Castle Rock, *Dunn & Harford* 1025 (NY); Klamath Falls, *Applegate* 738 (GH); Coast Mts., *Lloyd s.n.* (NY); Bonneville, *Palmer s.n.* (US); Tillamook, Wilson River, *Thompson* 3116 (DS, MO); N of Wilson River, SE of Blue Lake, 3300 ft, *Chambers* 4137 (OSC).

WASHINGTON: Cascades, *Dunn s.n.* (DS); Cascade Mts., *Tweedy* 340 (NY); Cascade Mts., Yakima Region, *Bandegee* 438 (NY, UC), *Tweedy s.n.* (NY); Olympic Mts., *Piper* 2226 (GH, US), *Piper s.n.* (WTU); Heart Lake, 4500 ft, *Dickinson* 62 (WTU). CHELAN Co.: Bridge Creek, Chelan Lake, 3000 ft, *Jones s.n.* (DS); Wenatchee National Forest, Chiwaukum Lake, *Eggleston* 13549 (US); Ice Creek, 6000 ft, *Morrill* 349 (WTU); Mt. Stuart District, Mt. Ingalls, *Eyerdam s.n.* (MO, UC); Bryan Butte, 6200 ft, *Ward* 51 (NY, WTU); Rainy Creek junction with Bridge Creek, *Ward* 633 (NY, WTU). CLALLAM Co.: Olympic Mts., *Elmer* 2305 (CAS, DS, MO, NY, ORE, WTU); Mt. Olympus, *Flett s.n.* (WTU); Mt. Angeles, 5000 ft, *Thompson* 5604 (DS, MO, WTU), 5000 ft, *Thompson* 7516 (MO, WTU), 4000 ft, *Thompson* 7843 (DS, GH, MO, WTU), 5300 ft, *Thompson* 10082 (NY, WTU), 6000 ft, *Howell* 7519 (CAS, DS), *Flett* 3352 (UC, US, WTU), *Webster s.n.* (WTU); Hoh River Trail to Hoh Lake, 3400 ft, *Otis* 1326 (WTU); Canyon Creek, 3000 ft, *Jones* 5910 (WTU), *Jones* 8368 (WTU), 3200 ft, *St. John* 4774 (GH, MO, UC, WTU); Bogachiel Mt., *Eyerdam* 6309 (WTU). JEFFERSON Co.: Constance Ridge, 4000 ft, *Thompson* 6569 (WTU); Lake Constance, 5500 ft, *Thompson* 7906 (WTU); Marmot Pass, 5000 ft, *Thompson* 9918 (MO, NY, WTU); Mt. Anderson, 5000 ft, *Meyer* 687 (MO,



WTU). KING Co.: Snoqualmie, *Smith s.n.* (MO, WTU); Snoqualmie Pass, Guy Peak, 3500 ft, *Thompson 9692* (NY, WTU); S ridge between Hester Lake & Godmeyer Hot Springs, 3500 ft, *Jones s.n.* (DAO). KITTITAS Co.: Martin to Lake Kichelas, *Henderson s.n.* (WTU); Yakima Valley, 2000 ft, *Wiegand et al. 522* (MO); Morse Creek, branch of American River, *Peirson 11853* (UC); Wenatchee Mts., Iron Peak, N Fork Teanaway River, *Kruckeberg 2583* (ID, NY, UC, WTU), DeRoux Forest Camp, *Kruckeberg 5314* (WTU). LEWIS Co.: Mt. Rainier National Park, *King s.n.* (CAS); Narada Falls, *Baker 743* (CAS), *Pope s.n.* (WTU); Silver Falls, Stevens Canyon, 2000 ft, *Utech 77-201* (CM); Goat Rocks Wilderness Area, Jordon Basin, 6150 ft, *Franklin 598* (OSC); Baldy Peak, 4000 ft, *Lamb 1322* (MO); Randle, W of Fawn Creek, *Spellenberg & Sutherland 1222* (HSC). MASON Co.: Mt. Elinor Trail, 2000 ft, *Freer 403* (WTU). OKANOGAN Co.: Okanogan Forest, Ashnola River, Sheep Mt. to Bald Mt. Trail, 1630 m, *Eggleston 13396* (US); Tiffany Range, Salmon Creek to Muckamuck Lookout, 4000 ft, *Thompson 6952* (DS, F, GH, MO, OSC, UC, WTU); Big Craggy, 3000 ft, *Thompson 10867* (CM, DS, MO, NY, WTU); Crescent Mine, W of Twisp, *Hitchcock & Muhllick 21595* (NY, WTU); N of Whistle Pass, NW of Conconully, 7200 ft, *Douglas 334* (DAO); Salmon Meadows Camp, NW of Conconully along Meadow Creek, 4500 ft, *Woodley 164* (GH); SE slope Mt. Chooaka, Cold Creek Camp, 6000 ft, *Kruckeberg 6543* (WTU). PIERCE Co.: Longmire Springs, *Wiegand et al. 523* (NY); White River to Owyhigh Lakes, 4500 ft, *Raven 8646* (CAS). SKAMANIA Co.: Cape Horn, *Howell s.n.* (GH), *Piper 4966* (US), *Gorman 2036* (ORE), *Suksdorf 10394* (WTU); Mt. Adams, Misery Gulch, *Lloyd s.n.* (NY); Spirit Lake, 3700 ft, *Meyer 770* (MO); Hamilton Mt., 1400 ft, *Detling 7065* (DS, ORE, UC). SNOHOMISH Co.: *Savage et al., s.n.* (MO); Whitechuck Mt., 3000 ft, *Eyerdam s.n.* (MO, UC); Mt. Pugh, 7000 ft, *Thompson s.n.* (WTU); Cascade Mts., Perry Creek Trail, 4000 ft, *Thompson 14746* (GH, MO, WTU). WAHKIAKUM Co.: Skamokawa, *St. John 8752* (WTU). WHATCOM Co.: Mt. Paddo, *Suksdorf s.n.* (DS, US); Goat Mt., 5500 ft, *Allen 233* (CAS, DS, GH, MO, NY, UC, US, WTU); Mt. Baker, *Gorman 2545* (ORE), 3700 ft, *Mason 3847* (GH, UC), *Mason 7414* (F, MO, NY, UC, WTU); E side Deming Glacier, 5500 ft, *Gorman 2893* (ORE); Meadow along Ruth Creek, *Muenschler 7713* (GH, UC); Austin Pass, 3000 ft, *Utech 78-300* (CM, WIS); Mt. Baker Lodge, 4000 ft, *Thompson 5370* (DS, WTU), *Thompson 5401* (DS, GH, WTU); Cliffs at Mt. Baker Lodge, 4200 ft, *Thompson 11011* (MO, WTU), *Thompson 11293* (WTU); N Fork Nooksack River, 3500 ft, *Benson 2401* (DS, MO, NY); Mt. Sauk, N of Rockport, 5000 ft, *Douglas 1308* (DAO).

#### DISCUSSION AND CONCLUSIONS

Based on the current northern hemisphere distribution, the genus *Stenanthium* has a pattern characteristic of descendant members of the so-called Arcto-Tertiary Geoflora. There is a wide-spread species in both eastern North America [*S. gramineum* (= *S. robustum*)] and western North America (*S. occidentale*; Fig. 1) as well as species in the central volcanic belt of Mexico (*S. frigidum*) and eastern Asia (*S. sachalinense*). The closely related *S. occidentale* and *S. sachalinense*, which is endemic to Sachalin Island, form a circum-northern Pacific disjunct pair. Their relationship will be investigated in this series.

The proposed segregation of *S. occidentale* and *S. sachalinense* into *Stenanthella* by Rydberg (1900) based largely on a superior ovary has not been accepted, nor has *Stenanthium rhombipetalum* Suksdorf (1923), a proposed robust segregate of *S. occidentale* with most open flowers male. As shown here, the flowering gynoecium is inferior, the flowers protandrous and the perianth epigynous. Zimmerman (1958) and Kupchan et al. (1961) proposed and used "for convenience in summarizing information only" Section *Eustenanthium* (*S. gramineum*) and Section *Stenanthella* (*S. occidentale*, *S. frigidum* and *S. sachalinense*).

Epigyny in *S. occidentale* is most evident in early anthesis because locule opening and ovule placentation occur well below the level at which the adnate perianth and stamens are freed. Within the epigynous zone, tepal, stamen and dorsal vasculature are only represented by peripheral compound or composite bundles. At maturity, the gynoecium is only slightly inferior.

The most common inflorescence in the Veratreae (*Melanthium*, *Zigadenus* and *Veratrum*) is a large polygamous panicle or compound raceme with the terminal flowers, especially on the side branches, staminate and those lower on the branches

perfect. *Stenanthium gramineum* and *S. frigidum* have this type, while the simple andromonoecious raceme of *S. occidentale* is among the most reduced in the tribe. Outbreeding within this raceme is facilitated by the protandrous flowers with dimorphic filaments and bilobed or v-shaped tepal nectaries. While *S. frigidum* is also reported to have tepal nectaries and *S. gramineum* not (Zimmerman, 1958; Kupchan et al., 1961), detailed comparison awaits future study. *Amianthium muscaetoxicum* (Utech, 1986) and several species of *Schoenocaulon* which lack nectaries are notable exceptions to the varying kinds of tepal nectaries and glands that are common throughout the Veratreae. The need to document carefully the relationships between inflorescence type and floral morphology and phenology in the Veratreae is important in future comparative work.

Three meiotic chromosome counts of  $n = 8$  have been reported for *S. occidentale* by Cave (1966, 1970) from Siskiyou County, California and Preece (1956) from Selway Falls, Idaho. The two other counts for the genus, both  $2n = 20$  for *S. gramineum* (= *S. robustum*) (Miller, 1930; Satō, 1942), need critical reexamination, since a  $x = 8$  base number is common among the Veratreae (Cave, 1970; Preece, 1956; Fedorov, 1969).

In describing the vascular floral anatomy and carpel morphology within the Veratreae, Anderson (1940), El-Hamidi (1952), Ambrose (1975, 1980), Sterling (1982) and Utech (1986) have noted characteristic similarities and differences. A common vascularization pattern consistently observed involves three compound vascular bundles composed of fused tepallary and staminal bundles (compound IT bundles or "zwischenbündel") and three compound bundles, similar to those above, fused to a dorsal bundle (compound OT bundle or dorsal-compound bundle). Major anatomical and morphological differences which are frequently used to differentiate genera (and species) include inflorescence type, floral geometry, tepal nectaries, presence or absence of sutural openings and a central carpellary hole at the lowermost level of ovular insertion, the degree of carpellary separation below the locular apex (an apocarpous tendency), the number of carpellary lateral or septal axial bundles and a hypogynous or perigynous versus an epigynous condition at the lowermost level of ovular insertion.

The complete pedicel to stigma vasculature of *S. occidentale* is derived through a complex series of divisions and fusions from three lower pedicel bundles. In the upper pedicel three compound OT bundles and three compound IT bundles are formed via tri-parted divisions which is typical of the Veratreae. Due to an inferior gynoecium and epigynous perianth, the tepallary, staminal and dorsal bundle formation is above the level at which the ventral and ovular supplies are established. Each tepal receives three bundles and the stamens one. There is no inter-connection between any of the tepal laterals or between laterals and medians. The ventral supply originates via successive divisions and fusions of continuing lateral branches following the compound IT bundle formation. Within each of the three undivided septal arms that subtend the locules in the epigynous zone, a fusion septal axial bundle with normally arranged xylem and phloem is associated with a compound ventral that divides into two ventrals. Each carpel receives a dorsal, two ventrals and a shared septal axial in the common septal arm. There is no terminal inter-connection between the ventrals and septal axials which end in the upper epigynous zone. Each of the two ventrals per carpel supplies two rows of bitegmic, basitropic, campylotropous ovules which develop into winged seeds.

Ambrose (1975) and Sterling (1982) reported two simple septal (axial) bundles

per septum and two to four accessory placental (ventral) bundles with some carpels having up to six or more in *S. gramineum* (= *S. robustum*) and that the septal bundles united with the placental bundles below the style. This, however, was not observed in *S. occidentale* where a shared fusion septal (SA) bundle and two placental (V) bundles occur without terminal fusion. That such inter-connection occurs in the Veratreae is known (Sterling, 1982; Utech, 1986), but which pattern occurs in the other species of *Stenanthium* remains to be investigated.

The occurrence in *S. occidentale* of an inferior gynoecium with an epigynous perianth at anthesis plus a weakly apocarpous fruiting gynoecium is a most unusual set of liliaceous characters. Furthermore, the insertion of freed floral parts as well as their vascularization formation is in a spiral pattern. Above the epigynous zone, the tepals are connate for a short vertical distance in which staminal epitepaly also occurs. A central carpellary hole at the gynoecium base is internally continuous with the three locules and the open stylar canal which is lined with non-papilloid cells. The three carpels are essentially free above the epigynous zone to the stylodium area. Carpellary separation along the inner septal margins results in septicidal dehiscence and dispersal of the winged seeds. No septal glands or nectaries were observed. Raphide idioblasts were not observed in carpellary or perianth tissue of *S. occidentale*. However, they were reported to be numerous in *S. gramineum* (= *S. robustum*) (Ambrose, 1975; Sterling, 1982) and occasional in *S. frigidum* (Sterling, 1982). The homogenous tannins which characterized the complete floral epidermis of *Amianthium muscaetoxicum* (Utech, 1986) were not observed in *S. occidentale*.

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RESULTS OF THE CARNEGIE MUSEUM OF NATURAL  
HISTORY EXPEDITIONS TO BELIZE.  
III. DISTRIBUTIONAL NOTES ON  
THE BIRDS OF BELIZE

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ABSTRACT

Much new information on the temporal and geographic distributions of the birds of Belize (Central America) has been gathered since the publication of Russell's (1964) monograph. We present here our data on bird distributions gathered during five expeditions to Belize from 1971 to 1985.

INTRODUCTION

Belize (until 1973 the British Crown Colony called British Honduras) has become in recent years an increasingly attractive area of Central America to students of ornithology. Relatively close to the United States, safe, English-speaking, and possessing a wealth of tropical life forms, it is, perhaps surprising that so little has appeared in print concerning the avifauna of the country. This may be explained in part by the high reputation enjoyed by Russell's (1964) excellent monograph on the distribution of the birds of the area. However, considerable additional fieldwork has been conducted in Belize in the past 20 years, yielding much new information on the distribution and status of the birds there.

Among the more important published records of Belizean birds since Russell's (1964) report are the annual Christmas Bird Counts (Young, 1973-1985) which cover two areas (Belize City and Belmopan) near the center of the country. Important additions have also been provided by Barlow et al. (1969, 1970, 1972), Erickson (1977), and Kiff and Kiff (1974). Several publications have reported the observations of British bird watching groups (Jenkins, [1983]; Hallchurch, 1982; Sherrard-Smith, 1982). A minimally annotated checklist (Weyer and Young, 1983) has recently been considerably revised and expanded by Wood et al. (1986). Other publications have dealt primarily with specific ornithological research projects in Belize (Kricher et al., 1984; Miller and Tilson, 1985; Orians, 1983; Stacey, 1981).

Representatives of the Section of Birds, The Carnegie Museum of Natural History, participated in two multidisciplinary expeditions to Belize in March-April 1984 and in June-July 1985. In addition, Leberman visited Belize on three other occasions between 1971 and 1983 in conjunction with fieldwork conducted in association with Manomet Bird Observatory. These five trips resulted in significant collections and observations of the country's avifauna. A primary objective during the 1984 and 1985 expeditions was to collect anatomical materials (skeletons and specimens preserved in alcohol). We preserved 858 specimens of

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191 species in alcohol and 839 specimens of 188 species as skeletons. For most of the skeletal preparations a spread feathered wing was also saved. In addition, we preserved 96 specimens of 73 species as traditional study skins; most of this latter group were either specimens in molt or species unusual to Belize. Also, our records include field observations of more than 350 species.

The purpose of this report is to comment on the distributions of the birds of Belize, especially where our observations supplement or modify Russell's (1964) findings. Thus, the accounts are presented below only for those species for which our information adds to or significantly changes what has already been reported in the literature.

### GAZETTEER OF LOCALITIES

Russell's (1964) monograph provided an extensive ornithological gazetteer for Belize, many sites of which were visited during the course of our own fieldwork. However, we also visited and collected at a number of sites not listed by him. The locations listed below are mentioned in the individual species comments (with one exception, Cubetas, which is a previously unidentified Russell location). Each site is identified by latitude and longitude and referenced to a location on a major world atlas (National Geographic Society, 1981), to identified sites on both the 1:750,000 Belize map (Directorate of Overseas Surveys, United Kingdom, 1981) and on the 1:50,000 topographic map series (quadrangles numbered 1–42; Directorate of Overseas Surveys, United Kingdom, 1966–1980), and to one of Russell's (1964) numbered gazetteer localities. These maps are referred to in the locality descriptions as NG Atlas, Belize map, Topo map (number), and Russell (number), respectively. Three sites are of camps set up by Carnegie Museum teams away from any named locality; each is identified as a CM camp.

- Altun Ha:** Belize District; 17°45'N, 88°21'W; marked on Topo map 11 and NG Atlas; 2 km W of Cowhead Creek (on old Northern Highway) on Belize map; 14 km S of Maskall (Russell 6); same location as Rockstone Pond (Barlow et al. 1969, 1970). This is an excavated Mayan ruin maintained as an archaeological preserve. The habitat is primarily heavy second growth forest with several large stands of cohune palms (*Orbignya cohune*). The area around the main temples is kept cleared of heavy vegetation. A small pond (cenote) surrounded by forest is situated near the excavated sites.
- Big Fall:** Toledo District; 16°15'N, 88°52'W; indicated on Belize map and Topo maps 38 and 42; 18 km N, 8 km W of Punta Gorda (NG Atlas); village at the crossing of the Southern Highway over the Rio Grande. Our collecting locality was 3 km SE of the bridge and on the south side of the river. This site is gallery forest along the river with mixed cultivation, milpa, huamil, and second growth forest away from the flood plain. This site should not be confused with another important birding locality, Big Falls, Belize District, a rice plantation 40 km W of Belize City on the Belize River, referred to by Barlow et al. (1972); Hallchurch (1982); Jenkins [1983], and others.
- Chaa Creek:** Cayo District; 17°07'N, 89°04'W; a private resort 5 km S of San Ignacio on the western bank of the Macal River (=Eastern Branch of the Belize River [Belize map]). The area is very hilly and much of the land has been cleared for pasture. A large stand of cohune palms is located just west of the resort property. Uncleared land is primarily young second growth forest.
- Chan Laguna:** Orange Walk District; 18°07'N, 88°29'W; a small fresh water lagoon and cattail marsh marked on Topo map 5; 3 km S, 1 km E of San Estevan (Belize map); 7 km E, 3 km N of Orange Walk Town (NG Atlas, Russell 2). The area was originally scrub forest but has largely been cleared for the growth of sugar cane.
- CM Bladen Camp:** Toledo District; 16°33'N, 88°43'W; point at which the Bladen Branch of the Monkey River exits the foothills of the Maya Mountains; 2 km NW of Chun Bank (Topo map 35); 12 km N, 1 km E of Medina Bank (Belize map); 26 km W, 22 km N of Monkey River Town (NG Atlas, Russell 85). This point is in the ecotone between the low savanna and the steep forested foothills. The elevation of the river at this site is approximately 40 m with the immediately adjacent hills rising to 140 m. Most of the forest is high second growth with a few very large trees remaining, especially around the site of an old sawmill.



- CM Chiquibul Camp:** Cayo District; 16°36'N, 89°00'W; elevation approximately 600 m; point where a new logging road south from Millionario and Grano de Oro Camp crosses the Chiquibul River; close to spot marked Moses Head Camp on Topo map 33; 12 km E, 11 km S of Round Hole Bank (Belize map); 60 km S, 5 km E of San Ignacio (NG Atlas); 16 km S, 1.5 km W of Millionario (Russell 73). The camp was in high forest with many large trees although much of the more valuable timber had selectively been removed.
- CM Columbia Forest Camp:** Toledo District; 16°17'N, 89°01'W; elevation approximately 140 m; 1 km N of site marked Forestry Camp on Topo map 37; 1.5 km E, 0.5 km S of Jimmy Cut (Belize map); 5 km N of San Antonio (NG Atlas); 7 km W, 2 km N of San Pedro Columbia (Russell 86). This area was originally high forest (well logged) but is now milpa and huamil (except for the steepest and rockiest hillsides) for a distance of 1–2 km from the main roads. Our collecting localities were largely at the edges of the huamil and into the forest.
- Coco Plum Cay:** Stann Creek District; 16°53'N, 88°07'W; marked on Belize map; 11 km E, 9 km S of Stann Creek Town [Dangriga] (NG Atlas); 4 km W of Tobacco Cay (Russell 60).
- Columbia Forest Station:** Toledo District; 16°17'N, 89°01'W; marked Forestry Camp on Topo map 37; 1 km S of CM Columbia Forest Camp (q.v.). Also called Salamanca, this site is now a military training camp.
- Cubetas:** Cayo District; 16°47'N, 89°02'W; marked on Topo map 28; 3 km N of Millionario (Russell 73). Mentioned by Russell in his text but not included in his gazetteer.
- The Dump:** Toledo District; 16°14'N, 88°57'W; marked on Topo map 42; 1 km WNW of junction of Southern Highway and Punta Gorda-San Antonio Road (Belize map, NG Atlas); considerable open marsh and wet meadow area traversed by the Punta Gorda-San Antonio Road (large quantities of fill had to be dumped there to make the road, hence the name). This has become a frequent stop for birdwatchers.
- Garbutts Cay:** Stann Creek District; 16°59'N, 88°05'W; marked on Belize map; 14 km E of Stann Creek Town [Dangriga] (NG Atlas); 13 km N of Tobacco Cay (Russell 60).
- Guanacaste Park:** Cayo District; 17°16'N, 88°46'W; park on the banks of the Belize River and Roaring Creek at the junction of the Western and Hummingbird highways; just east of the town of Roaring Creek. The park is mostly second growth forest.
- Jimmy Cut:** Toledo District; 16°17'N, 89°02'W; marked on Topo map 37 and Belize map; 6 km N, 1 km W of San Antonio (NG Atlas). Formerly high forest, all areas near roads are now milpa.
- Las Lomitas:** Toledo District; 16°29'N, 88°35'W; fire lookout station 3 km S, 2 km W of junction of the Southern Highway and the Swasey Branch of the Monkey River (Belize map); 17 km NW of Monkey River Town (NG Atlas, Russell 85). This is an area of low hills covered in pine forest—pine savanna with dense brush along the waterways.
- Milepost 24–30:** Western Highway: Belize District; 17°22'N, 88°32'W (Milepost 30); 24 km E, 12 km N of Belmopan. An old stretch of the original Western Highway parallels the present highway to the south between these mileposts; this old road is passable for most of its length and is used as access for several properties. The area between the old and new highways is mostly pine savanna and includes a fairly extensive grass and sedge marsh near Milepost 24. Our collecting sites were primarily between the old and new highways.
- Salamanca:** Toledo District; Alternate name for Columbia Forest Station (q.v.).
- Union Camp:** Toledo District; 16°24'N, 89°09'W; elevation 720 m; marked on Topo map 37; just SW of Little Quartz Ridge (Belize map); 16 km N, 11 km W of San Antonio (NG Atlas). This camp was visited by the Royal Air Force group (see below; Jenkins, [1983]).

### SPECIES ACCOUNTS

Within each of the accounts, localities are either as described above or are keyed to identified sites in the National Geographic Atlas (National Geographic Society, 1981), or to sites on the 1:750,000 Belize map (Directorate of Overseas Surveys, United Kingdom, 1981).

Three organized groups are mentioned in several of the following accounts: The [British] Royal Air Force Ornithological Society mounted an expedition to Belize from February through April 1981; their records, summarized in an extensive report (Jenkins, [1983]), are credited to the RAFOS. Also included in this report is a summary of mist-netting at several locations from April through June 1979. The [British] Army Bird Watching Society mounted an expedition to Belize during February and March 1982, and published their records in a journal of very limited

distribution (Hallchurch, 1982); their sightings are credited to the ABWS. Several groups connected with Manomet Bird Observatory have participated in banding operations in Belize; their observations are credited to the Manomet group or to Mrs. Erma J. Fisk who organized the first two trips.

The classification and nomenclature used in this report follow the sixth edition of the *Check-list of North American birds* and supplement (American Ornithologists' Union, 1983, 1985). Specimens listed are in the collections of The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. The state of preparation of a specimen may be inferred from the catalog number given: A = complete specimen stored in alcohol; P = study skin; S = skeleton, usually with an associated spread feathered wing.

#### TINAMOUS—TINAMIDAE

##### Thicket Tinamou, *Crypturellus cinnamomeus*

One seen at close range in pine savanna habitat in Orange Walk District near the new Northern Highway just north of the Belize District line, 1 July 1985. Very few records of Thicket Tinamou exist for Belize. Russell (1964) listed the species as uncommon near Hill Bank (approximately 45 km SW of the present locality) in dense second growth forest and rare near Gallon Jug, also in forest. No other published records are available; the status listed in Wood et al. (1986) reflects Weyer's belief that the species occurs (very rarely) in the southern hardwood forests of the country and in the Mountain Pine Ridge.

#### GREBES—PODICIPEDIDAE

##### Pied-billed Grebe, *Podilymbus podiceps*

One seen on Crooked Tree Lagoon, 11 June 1985; one seen on Chan Laguna, 27 June 1985. Although Pied-billed Grebes are common winter residents throughout much of Belize, few summer records exist. Russell (1964) listed only two, both from May. The present records further support the belief that this species breeds in Belize. Monroe (1968) reported breeding of Pied-billed Grebes in Honduras.

#### CORMORANTS—PHALACROCORACIDAE

##### Olivaceous Cormorant, *Phalacrocorax olivaceus*

Common throughout Belize except on the cays. Records include: one collected (CM-A3837) of three seen on the Sibun River just north of the Hummingbird Highway bridge, 20 March 1984; two seen repeatedly near the CM Bladen Camp, 3–7 April 1984; two seen 5 km south of San Ignacio on the Macal River (Eastern Branch, Belize River), 16 June 1985; two seen repeatedly near the Guacamallo Bridge on the Macal River, 23–24 June 1985. Russell (1964) lists relatively few records for the country. The RAFOS also reported these birds to be common, and saw large numbers (50) on Cay Chapel.

#### ANHINGAS—ANHINGIDAE

##### Anhinga, *Anhinga anhinga*

One seen flying over savanna at Milepost 29, Western Highway, 19 February 1983. One seen repeatedly at Chan Laguna, 28–30 June 1985. Russell (1964) lists few records for Belize. The RAFOS recorded up to 30 at Northern Lagoon and

many elsewhere; the ABWS recorded four to six daily at Big Falls and the Airport Camp.

FRIGATEBIRDS—FREGATIDAE

Magnificent Frigatebird, *Fregata magnificens*

A very common species along the coast and on the cays, these birds occasionally stray inland: one was seen at Milepost 29 on the Western Highway, 4 July 1985.

BITTERNS AND HERONS—ARDEIDAE

Pinnated Bittern, *Botaurus pinnatus*

Breeding male collected (CM-S8655; testes  $25 \times 12$  mm) at Milepost 21 on the Western Highway, 14 March 1984; non-breeding male found dead by Dora Weyer (CM-S10296; flat skin and skeleton; testes 9.2 mm), Milepost 14 on the Northern Highway, 21 April 1985; two seen several times at Milepost 24 on the Western Highway, July 1985. All records were from open savanna, especially marshy areas. This species is cryptic and difficult to observe. Wood flushed the specimen collected in 1984 from a distance of less than 10 m; it was unseen until it flew. In addition, these birds appear to be restricted to a habitat not usually frequented by birders. This, perhaps, accounts for the lack of published records for the country: Russell (1964) did not list the species (although he mentions Yucatan records). The first record and specimen for Belize was one found by Dora Weyer in 1970, also in savanna habitat (Barlow et al. 1972). Two were also seen during the 1982 Belize City Christmas Bird Count (Young 1973–1985). The bitterns seen by the ABWS (1982) at Big Falls (as many as five in one day) were probably this species. We feel certain that Pinnated Bitterns are much less rare than the records indicate; additional fieldwork is needed in wet savanna habitats.

American Bittern, *Botaurus lentiginosus*

One wing salvaged by Meg Price Craig (CM-P144864) from a bird shot by a local hunter near Mussel Creek (approx. 25 km WNW Belize City) in early February 1972. This is the first specimen record of this bittern for Belize; Russell (1964) listed two sight records. The bittern reported by the ABWS (1982) from The Dump may also have been this species.

Least Bittern, *Ixobrychus exilis*

Female collected (CM-S10235; largest ovum 6 mm) at Chan Laguna, 29 June 1985. Russell (1964) listed only two records: a transient collected on Half Moon Cay and a winter sight record for Hill Bank. Both the ABWS and RAFOS recorded at least three within 25 km of Belize City. Weyer (personal communication) has observed this species several times in fresh water lagoons along the coastal plain. We consider it to be an uncommon and local permanent resident with a small augmentation of winter visitors from the north.

Bare-throated Tiger-Heron, *Tigrisoma mexicanum*

Common in coastal pine ridges, especially in the wetter areas, but somewhat secretive. Among our records is one of four birds repeatedly seen in a marsh near Milepost 24 of the Western Highway, 26 June to 4 July 1985. This species is listed as uncommon in northern forests by Russell (1964). Between one and 10 have been seen on all but two Belize City Christmas Counts (Young, 1973–1985).

Great Blue Heron, *Ardea herodias*

One found dead (CM-S8644) in the Belize River near Burrell Boom, 5 March 1984, is the first specimen of the species for Belize. One seen at Crooked Tree Lagoon, 11 June 1985; one seen at Milepost 24 of the Western Highway, 26 June 1985. No previous published records exist for the period June through October, although Weyer (personal communication) believes that a few breed each year on the northern cays. Griscom (1926) found the species breeding on the Culebra Keys, Quintana Roo, in January 1925.

Great Egret, *Casmerodius albus*

An estimated 1200 seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) reported no documentation of breeding, but the present record strongly suggests that these birds nest in the country. Breeding is also to be expected since it has been reported from surrounding countries (Monroe, 1968; Paynter 1955).

Snowy Egret, *Egretta thula*

An estimated 100 seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed no records for June.

Little Blue Heron, *Egretta caerulea*

An estimated 250 seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed no records for the period 15 May–19 July. Weyer (personal communication) has recorded this species breeding on the northern cays.

Tricolored Heron, *Egretta tricolor*

Three seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed no records for June or July.

Reddish Egret, *Egretta rufescens*

Two seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed only one sight record and Kiff and Kiff (1974) reported the first specimen for the country. The ABWS (1982) recorded two on Cay Chapel. Weyer (personal communication) has recorded this species breeding on two northern cays.

Cattle Egret, *Bubulcus ibis*

Abundant throughout the country in suitable habitat. Russell (1964) listed only a few records and thought that the species had only just become established as breeding birds at that time.

Green-backed Heron, *Butorides striatus*

An estimated 25 seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed no June or July records and knew of no breeding records although he believed it to nest.

Black-crowned Night-Heron, *Nycticorax nycticorax*

Three seen along Black Creek (near Crooked Tree Lagoon), 5 March 1984; two seen at Sand Hill, Belize District, 9 March 1984. Russell (1964) considered this species to be a rare transient and winter resident and listed only four records. However, we consider the bird to be fairly common; Young (1973–1985) recorded the species in most years for the Belize City Christmas Count (2–13 individuals per count) and both the RAFOS and ABWS encountered several birds. Weyer

(personal communication) believes some individuals may remain throughout the summer months.

IBISES AND SPOONBILLS—THRESKIORNITHIDAE

White Ibis, *Eudocimus albus*

Eight seen near Sand Hill, Belize District, 17–19 March 1984; 15 seen just west of Dangriga Airport, 21 March 1984; 200 seen at Crooked Tree Lagoon, 11 June 1985; small numbers seen repeatedly southwest of Belize City flying over the mangroves, 11 June–8 July 1985. Russell (1964) stated that there were no recent records of White Ibis for Belize. However, Erickson (1977) found 10 near Dangriga on 26 December 1976 and Young (1973–1985) listed the species for the first three Belize City Christmas Counts. Our records, those of the RAFOS and ABWS (up to 100 individuals per day), and records from more recent Christmas Counts (244 recorded on the 1983 Belize City count), suggest that these birds are increasing in numbers in Belize.

Roseate Spoonbill, *Ajaia ajaja*

Fifteen seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed only two records for the country. Young (1973–1985) recorded one bird on the Belize City Christmas Count in 1983 and again in 1984. The RAFOS recorded three just outside of Belize City. These birds are probably more common than the records indicate, but may be largely confined to the northeastern part of the country.

SWANS, GEESE AND DUCKS—ANATIDAE

Black-bellied Whistling-Duck, *Dendrocygna autumnalis*

Six seen at Crooked Tree Lagoon, 11 June 1985; two seen Milepost 29 on the Western Highway, 27 June 1985; two seen at Chan Laguna, 30 June 1985. Russell (1964) considered this species rare in Belize but remarked that it seemed to be increasing. Subsequent published notes (Barlow et al., 1969, 1972) and conversations with Dora Weyer and others in Belize, as well as our own observations, suggest that the species is now relatively common in the northern half of the country.

KITES, EAGLES, HAWKS AND ALLIES—ACCIPITRIDAE

Hook-billed Kite, *Chondrohierax uncinatus*

One seen each date at Columbia Forest Station, 5 December 1971 (Leberman and K. S. Anderson), 25 March 1972 (Leberman). Russell (1964) listed only two records for this rare hawk, neither from the southern forests. The only other published records are from the Belmopan Christmas Counts (Young, 1973–1985): one seen in 1982 and one in 1984.

Double-toothed Kite, *Harpagus bidentatus*

One seen along Hummingbird Highway northwest of Caves Branch, 23 February 1983 (Leberman and Manomet group); male collected (CM-S8722; testes  $8 \times 4.5$  mm) 1 km north of Columbia Forest Station, 22 March 1984. The only other published records for this species in Belize are one in Russell (1964) and two from the Belmopan Christmas Counts (Young, 1973–1985): one seen in 1978 and three in 1980.

Solitary Eagle, *Harpyhaliaetus solitarius*

One seen soaring above Guacamallo Bridge, 24 June 1985. Russell (1964) does not list this species for Belize. Weyer (personal communication) indicates that the bird we saw is probably one of a pair that has nested near Guacamallo Bridge for the past several years.

Broad-winged Hawk, *Buteo platypterus*

One captured, photographed (photo on file at CM) and released along the Hummingbird Highway south of Belmopan, 24 February 1983 (Leberman and Manomet group). The only other published records for this very rare transient (and winter visitant?) are the specimen (taken 22 October 1906) mentioned by Russell (1964) and one bird seen on the 1973 Belize City Christmas Bird Count (Young, 1973–1985). Broad-wings should be looked for during the fall since they migrate through Central America in large numbers (Monroe, 1968).

Swainson's Hawk, *Buteo swainsonii*

One seen at Caves Creek, 23 February 1983 (Leberman and Manomet group); one seen soaring over CM Columbia Forest Camp each day, 23–24 March 1984; one seen along Hummingbird Highway, 6 April 1984 (Manomet group). This species is not listed for Belize by Russell (1964), but has been frequently recorded (1–4 individuals) on both Belizean Christmas Counts (Young, 1973–1985).

Red-tailed Hawk, *Buteo jamaicensis*

One immature seen flying at close range just northwest of Belize City, 16 March 1984. Russell (1964) listed only Mountain Pine Ridge records. The only other published record is of one seen on the 1981 Belmopan Christmas Count (Young, 1973–1985).

Harpy Eagle, *Harpia harpyja*

One immature seen in high forest northwest of Columbia Forest Station near Jimmy Cut by Leberman and K. S. Anderson, 28 March 1972. The only other published record is from Gallon Jug (Russell, 1964).

Black-and-white Hawk-Eagle, *Spizastur melanoleucus*

One seen perched at Beaver Dam Creek (near Milepost 38 of the Western Highway, Cayo District), 25 March 1984 (Manomet group); one seen at the CM Bladen Camp, 3 April 1984; one seen at Milepost 29 of the Western Highway, 26 June 1985; one seen at Milepost 24 of the Western Highway, 3 July 1985 (the latter two records are likely of the same bird). This rare hawk seems to prefer the forest edge. Russell (1964) lists only three records but the species has also been seen three times on the Belmopan Christmas Counts (Young, 1973–1985).

Black Hawk-Eagle, *Spizaetus tyrannus*

One seen flying over Altun Ha, 18 March 1984. Black Hawk-Eagles are the most common of the three hawk-eagles in Belize despite the single record of Russell (1964); one or two individuals have been recorded on most of the Belmopan Christmas Counts and the species has also been recorded twice on the Belize City Christmas Count (Young, 1973–1985). Erickson (1977) saw one near Belmopan and the RAFOS recorded two in the Columbia Forest region. The present sighting is farther north than other published records for Belize; we think this species could be encountered anywhere in the forested regions of the country.

### Ornate Hawk-Eagle, *Spizaetus ornatus*

One seen at Milepost 30 of the Western Highway, 19 February 1983 (Leberman); one seen over the Sibun River southeast of Milepost 36 on the Western Highway, 5 July 1985. Although Russell (1964) considered this species as merely uncommon we think the birds quite rare and even less frequent than Black Hawk-Eagles. Ornate Hawk-Eagles have been recorded only once (Belmopan, 1984) on the Christmas Counts (Young, 1973–1985). The present records support Russell's observation that they occasionally forage in pine savannas, away from hardwood forests.

## CARACARAS AND FALCONS—FALCONIDAE

### Barred Forest-Falcon, *Micrastur ruficollis*

One seen CM Bladen Camp, 7 April 1984; breeding adult female (CM-S9081; ovaries  $14 \times 7$ ,  $16 \times 8$  mm) collected near Rio Frio Cave, Augustine, Cayo District, 16 April 1984; immature molting into adult plumage captured, photographed and released at Guacamallo Bridge, 24 June 1985; one seen near San Estevan, Orange Walk District, 29 June 1985. This secretive falcon is undoubtedly more common than the few published records in Russell (1964) indicate. Most of our encounters with the species occurred when the falcon was attracted by struggling mist-netted birds.

### Applomado Falcon, *Falco femoralis*

At least five individuals seen hunting through smoke of a pine savanna fire near Milepost 29 of the Western Highway, 31 March 1984 (Manomet group); one seen at Las Lomitas, 9 April 1984; two seen in pine forest 4 km N and 1.5 km W of Melinda Forest Station, 19 June 1985. We consider this species to be more common in Belize than reported by Russell (1964). Young (1973–1985) has reported sightings for five of the Belize City Christmas Counts.

### Orange-breasted Falcon, *Falco deiroleucus*

Adult and two immatures seen at close range sitting together in a dead snag near our CM Chiquibul Camp, 21 June 1985. Haney (1983) recorded this rare falcon not far north of our site and several other observations of these birds have been made in the Chiquibul in the past few years (Weyer, personal communication); the species apparently breeds in this area. The RAFOS encountered one individual at Lubaantun, the Maya ruin near San Pedro Columbia, 4 April 1981. These are the only published records of the species from Belize.

## RAILS, GALLINULES AND COOTS—RALLIDAE

### Common Moorhen, *Gallinula chloropus*

Two seen at Crooked Tree Lagoon, 25 February 1983 (RCL and Manomet group); 20 seen at Sand Hill, Belize District, 9 March 1984; two seen on the New River at Orange Walk Town, 30 June 1985. Russell (1964) reports only a few sight records for this species. However, Barlow et al. (1969) reported three specimens taken from Rockstone Pond in April, Erickson (1977) noted the species between Belize City and Orange Walk in December, and Young (1973–1985) recorded them (sometimes in considerable numbers) on the Belize City and Belmopan Christmas Counts. The present summer record suggests these birds occur throughout the year, as they do in Honduras (Monroe, 1968).



## PLOVERS——CHARADRIIDAE

Black-bellied Plover, *Pluvialis squatarola*

Two or three seen on Tobacco and Coco Plum cays, 11–12 March 1984. Russell (1964) lists only three records for the country but Young (1973–1985) records the species on all Belize City Christmas Counts except two and the RAFOS and ABWS found them at Belize City, Dangriga and Cay Chapel. This species is probably common on the cays during winter and migration periods.

Wilson's Plover, *Charadrius wilsonia*

Two seen and photographed on Garbutt's Cay, 10 March 1984. Russell (1964) lists very few records but Barlow et al. (1969) cite a number of additional records and specimens. The RAFOS encountered single birds at Dangriga and Punta Gorda, and the ABWS encountered 40 on Cay Chapel.

## STILTS AND AVOCETS——RECURVIROSTRIDAE

Black-necked Stilt, *Himantopus mexicanus*

Approximately 80 seen at Crooked Tree Lagoon, 27 March 1984 (Manomet group); six seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed only three records for Belize, all from spring, and Young (1973–1985) recorded the species on three Belize City Christmas Counts. The RAFOS and ABWS recorded considerable numbers (up to 40) in the Belize City area. Weyer (personal communication) reports that the species has been found nesting within the country in recent years.

## SANDPIPERS AND ALLIES——SCOLOPACIDAE

Greater Yellowlegs, *Tringa melanoleuca*

Two seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed very few records for this species, all from the period August–March. It was unrecorded on the Christmas Counts until December 1983 when 15 were seen in Belize City (Young, 1973–1985). The RAFOS and ABWS recorded the species from Big Falls Ranch.

Lesser Yellowlegs, *Tringa flavipes*

Four seen at Sand Hill, 9 March 1984. Russell (1964) listed very few records for this species (all from the period February–March) and it has been recorded only four times on the Christmas Counts (Young, 1973–1985). However, the RAFOS and ABWS encountered as many as 60 at a time at Big Falls Ranch.

Willet, *Catoptrophorus semipalmatus*

Four seen at Dangriga, 20 March 1984. Russell (1964) listed very few records for this species and it has been recorded only twice on the Christmas Counts (Young, 1973–1985). Erickson (1977) noted it at Belize City and Dangriga in December. The RAFOS and ABWS recorded small numbers at many coastal localities and on Cay Chapel.

Upland Sandpiper, *Bartramia longicauda*

Female collected (CM-P162522; ovary  $9 \times 5$  mm) of two of this species seen in dry savanna just south of the CM Bladen Camp. This is the first published record in Belize since 1889 (Russell, 1964) but small numbers undoubtedly stop each year during migration; additional fieldwork is needed in grassland areas.



Long-billed Curlew, *Numenius americanus*

One seen in flight (cinnamon wing linings and enormous bill clearly visible) at Dangriga, 21 March 1984. This is the first published record for Belize but the species has been noted occasionally in the past (Weyer, personal communication). Belize is near the southern limit of the winter range of this species (American Ornithologists' Union, 1983).

SKUAS, GULLS, TERNS AND SKIMMERS—LARIDAE

Caspian Tern, *Sterna caspia*

Five seen at Crooked Tree Lagoon, 11 June 1985. Russell (1964) listed only three records and Erickson (1977) added a fourth (at Dangriga) but Young (1973–1985) recorded the species on every Belize City Christmas Count (as many as 32 individuals) except two.

Sandwich Tern, *Sterna sandvicensis*

Ten seen just north of Belize City, 9 March 1984. Erickson (1977) summarized the few records for Belize to that time. The RAFOS and ABWS encountered this species frequently along the coast and considered it common.

PIGEONS AND DOVES—COLUMBIDAE

Red-billed Pigeon, *Columba flavirostris*

Two to five seen at Chaa Creek each day, 20–23 April 1984; two collected (CM-A4458, 4485) at Chaa Creek, 21 and 23 April 1984; four collected (male, 2 females, immature female; CM-S10051, 10052, 10053, 10054) of at least 40 seen at Chaa Creek, 16 June 1985. Russell (1964) listed only one record (Corozal). Barlow et al. (1970) listed several records from Rockstone Pond and Erickson (1977) noted one near Dangriga. This species has been recorded on most Belize City Christmas Counts and twice on the Belmopan count (Young, 1973–1985). The RAFOS also recorded several individuals at Guacamallo Bridge. Despite the scarcity of records from the western part of the country, it was the commonest pigeon in the Chaa Creek area. This species deserves more attention in Belize since it is considered rare elsewhere on the Caribbean slope of Central America (American Ornithologists' Union, 1983).

White-tipped Dove, *Leptotila verreauxi*

Common in the northern half of the country; specimens from Milepost 30 of the Western Highway, Chaa Creek, Chan Laguna. Russell (1964) listed only two records and Barlow et al. (1969) reported on three specimens from the Rockstone Pond area. Young (1973–1985), however, has noted the species on every Christmas Count (both Belize City and Belmopan) except one. This dove appears to be largely absent from the southern half of Belize, the only record being one sighting by the RAFOS in the Columbia Forest area (Aguacate).

CUCKOOS AND ALLIES—CUCULIDAE

Striped Cuckoo, *Tapera naevia*

One seen near San Antonio, Toledo District, 4 December 1971 (Leberman, K. S. Anderson, D. Weyer); one seen near Milepost 29 of the Western Highway, 17 and 27 February 1983 (Leberman and Manomet group); one seen near Milepost 33 of the Western Highway, 21 March 1984 (Manomet group). Russell (1964)

noted only two records of this very shy species. Young (1973–1985) listed the species on five of the Belmopan Christmas Counts.

#### TYPICAL OWLS——STRIGIDAE

##### Vermiculated Screech-Owl, *Otus guatemalae*

Two nestlings brought by a local Indian to Columbia Forest Station, March 28 1972, and subsequently released; one heard at CM Columbia Forest Camp, 26 March 1984; rufous phase male found dead on road (CM-P162528; testes  $5 \times 3$  mm) at Milepost 36 of the Western Highway (Cayo District), 4 April 1984. This latter bird is the first specimen of the species for Belize. The only other published records are two sightings noted by Russell (1964), one bird reported on the 1981 Belmopan Christmas Count (Young, 1973–1985), individual birds heard by the RAFOS north of Guacamallo Bridge and in the Columbia Forest, and two birds mist-netted in the Columbia Forest (Jenkins, [1983]).

##### Least Pygmy-Owl, *Glaucidium minutissimum*

Immature found dead (CM-P162527; ovary(?)  $3 \times 2$  mm) in Belmopan, 23 March 1984; one mist-netted and photographed east of the Sibun River (in Belize District) southeast of Milepost 35 on the Western Highway, 14 April 1984 (Manomet group); two to four seen each day at Chaa Creek, 20–23 April 1984; two of these were seen copulating near their presumed nest hole on 21 April. Russell (1964) listed only one other record for the country.

##### Ferruginous Pygmy-Owl, *Glaucidium brasilianum*

Non-breeding male (testes  $3 \times 2$  mm; CM-S10251) collected in Orange Walk District near the new Northern Highway 0.5 km N of the Belize District line, 1 July 1985. Russell (1964) listed few records outside of the Mountain Pine Ridge but this species is widespread and fairly common in Belize.

##### Stygian Owl, *Asio stygius*

One photographed by Ford Young at Milepost 15 of the Western Highway (near Hattieville), 8 November 1971 (*vide* K. S. Anderson); one seen at Milepost 30 of the Western Highway, March 1983 (Manomet group); one found dead on road (CM-A5210) by Dora Weyer at Milepost 30 of the Western Highway, 10 March 1986. Only one published record exists for Belize, a bird collected in the Mountain Pine Ridge (Russell, 1964).

#### SWIFTS——APODIDAE

##### Chimney Swift, *Chaetura pelagica*

Female (CM-P162504; ovary  $3.5 \times 4$  mm) collected from a flock of approximately 100 swifts 3 km SE of Big Fall, Toledo District, 29 March 1984. This and similar flocks seen in the same area on 30 March and 1 April contained both Chimney and Vaux's (*C. vauxi*) swifts (as well as two Lesser Swallow-tailed Swifts); on 30 March at least six Chimney Swifts were present. The size difference between the two *Chaetura* species was quite obvious. Russell (1964) doubted the validity of the two alleged records of Chimney Swift for Belize. However, the Chimney Swift clearly migrates through the country, at least occasionally. Young (1973–1985) has recorded a few individuals in the past several years on Christmas Counts. Monroe (1968) considered this species an uncommon to common fall migrant and common spring migrant in the coastal lowlands of Honduras.

Lesser Swallow-tailed Swift, *Panyptila cayennensis*

Two seen in the large flock of swifts noted above on 30 March. Russell (1964) considered the species regular and probably nesting at Gallon Jug, but there are few records from elsewhere in Belize.

HUMMINGBIRDS—TROCHILIDAE

Band-tailed Barbthroat, *Threnetes ruckeri*

Two mist-netted Columbia Forest Station, 6, 14 December 1971 (E. J. Fisk); male (CM-P162501, testes  $2.5 \times 2$  mm) collected at CM Columbia Forest Camp, 24 March 1984; male and two of unknown sex (CM-S8787, testes 2.2 mm; CM-A3956; CM-A3977) collected at CM Columbia Forest Camp, 25 March 1984; male (CM-P162506, testes  $2.5 \times 2$  mm) collected 3 km SE of Big Fall, Toledo District, 29 March 1984. Barlow et al. (1972) reported the first record of this species for the country. The RAFOS and the ABWS mist-netted several in the Columbia Forest area. Our experience indicates that this species is not particularly rare in the southernmost parts of Belize.

Scaly-breasted Hummingbird, *Phaeochroa cuvierii*

One mist-netted at the Columbia Forest Station, 9 December 1971 (E. J. Fisk et al.); one collected (CM-A3905) at CM Columbia Forest Camp, 23 March 1984; one collected (CM-A4126) 3 km SE of Big Fall, Toledo District, 31 March 1984; two collected (CM-S8963 female, ovary  $4 \times 4$  mm; CM-A4971) at the CM Bladen Camp, 4, 5 April 1984. Russell (1964) reported only a few records of this inconspicuous hummingbird, all from the northern half of the country. However, the RAFOS and ABWS each mist-netted one in the Columbia Forest area. The present records indicate that it is at least as common in the south and perhaps more so than in the northern forests.

Wedge-tailed Sabrewing, *Campylopterus curvipennis*

One non-breeding male collected (CM-S8998, testes  $<1$  mm) of several seen at the CM Bladen Camp, 6 April 1984; one collected (CM-A4971) of five seen 6 km S, 6 km W of Progreso, Corozal District, 30 June 1985; several others collected at localities covered by Russell (1964). Russell was the first ornithologist to record this species in Belize; he considered it "moderately common" but local, whereas we found it nearly everywhere there was hardwood forest. However, despite their concentration on hummingbirds, neither the RAFOS nor the ABWS encountered this species. Hutson and Lyal mist-netted seven in the Columbia Forest area (Jenkins, [1983]).

Crowned Woodnymph, *Thalurania colombica*

Three collected (CM-P162502, male, testes  $<1$  mm; CM-S8777, male, testes  $2 \times 1.5$  mm; CM-A3951) at CM Columbia Forest Camp, 24, 25 March 1984. Russell (1964) reported only one record for Belize, a male taken near our locality. The RAFOS and ABWS each mist-netted one individual in the Columbia Forest area and Hutson and Lyal also netted two individuals there (Jenkins, [1983]).

Buff-bellied Hummingbird, *Amazilia yucatanensis*

Male collected (CM-P166042, testes  $3 \times 1.5$  mm) 3 km N, 1 km W of the Melinda Forest Station; male collected (CM-S10269, testes  $1 \times 0.5$  mm) 1.5 km east of Milepost 29 of the Western Highway; one seen at close range near Chan

Laguna, 30 June 1985. Russell (1964) listed only a few records, all from the lowland pine ridges. Our localities are all lowland but only one was in pines (Milepost 29 of the Western Highway). The Melinda Forest Station bird was taken in an island of broadleaf forest along Big Creek, surrounded by pine ridge. The Chan Laguna sighting was from northern hardwood forest remnants in an area dominated by sugar cane plantations.

Stripe-tailed Hummingbird, *Eupherusa eximia*

Female collected (CM-P144851) by D. Weyer, E. J. Fisk et al. at the Columbia Forest Station, 6 December 1971. This species was previously recorded only from the Cockscomb Mountains (Russell, 1964) and from Union Camp by the RAFOS; the present record is the first for the lowlands of Belize.

TROGONS—TROGONIDAE

Collared Trogon, *Trogon collaris*

Male captured, photographed and released near Rio Frio Cave, Augustine, Cayo District, 15 April 1984; at least three males and one female seen and heard near the CM Chiquibul Camp, 21 June 1985. Russell (1964) listed only five records for the country; the RAFOS added one record from the Columbia Forest area (Aguacate). This species appears to be quite rare north of the Mountain Pine Ridge and southeast of the Maya Mountains. However, in the Chiquibul it appears to be somewhat more common.

MOTMOTS—MOMOTIDAE

Tody Motmot, *Hylomanes momotula*

One captured, photographed and released of two seen repeatedly 1 km S of the Guacamallo Bridge, 23, 24 June 1985. Russell (1964) listed few records for Belize of this uncommon bird.

TOUCANS—RAMPHASTIDAE

Emerald Toucanet, *Aulacorhynchus prasinus*

Female collected (CM-P166050, ovary  $11 \times 7$  mm) 12 km S, 1 km W of Millionario, 22 June 1985. Russell (1964) considered this species very uncommon. The largest populations may occur in the Chiquibul region.

WOODPECKERS—PICIDAE

Red-vented Woodpecker, *Melanerpes pygmaeus*

One adult and one immature male collected (CM-P166064, testes  $5 \times 3$  mm; CM-P166065, testes  $1.5 \times 1$  mm) of at least five seen west of Chan Laguna, 29 June 1985. Russell (1964) listed only two records, but the species has subsequently been reported by Barlow et al. (1969), Erickson (1977), and on two recent Belize City Christmas Counts (Young, 1973–1985). All encounters have been in the coastal lowland forests from Belize City north. We believe this species to be more common than the published records indicate, although restricted to the northeastern portion of the country, an area that has received relatively little ornithological investigation. The birds we encountered were in remnant patches of hardwood forest surrounded by sugar cane plantations.

Ladder-backed Woodpecker, *Picoides scalaris*

Female collected (CM-A3860) at Las Lomitas, 21 March 1984; one seen at close range in Orange Walk District 0.5 km N of the Belize District line near the new Northern Highway, 1 July 1985. The March record lies well within the species' range as described by Russell (1964). However, the July record considerably extends to the north the known range of this woodpecker in Belize, narrowing the gap between the Belize and Yucatan populations.

OVENBIRDS—FURNARIIDAE

Scaly-throated Leaf-tosser, *Sclerurus guatemalensis*

Two banded at the Columbia Forest Station, one each day, 13 December 1971 and 24 March 1972 (Manomet group); three collected (male, CM-S8769; female, CM-S8771; unknown sex, CM-A3949) at the CM Columbia Forest Camp, 24–25 March 1984. Russell (1964) listed few records for this elusive species and only one additional sighting has been published: Hutson and Lyal netted one bird in the Columbia Forest area (Jenkins, [1983]). Our specimens were mist-netted at the edge of high forest bordered by huamil.

WOODCREEPERS—DENDROCOLAPTIDAE

Strong-billed Woodcreeper, *Xiphocolaptes promeropirhynchus*

Male collected (CM-S8794: testes  $10 \times 6$  mm) at CM Columbia Forest Camp, 25 March 1984 in high forest. Russell (1964) listed very few records and none from the southern parts of the country. This species probably occurs in very low numbers wherever extensive high forest remains.

Streak-headed Woodcreeper, *Lepidocolaptes souleyetii*

Male collected (CM-S8953: testes  $12 \times 7$  mm) of two seen at the CM Bladen Camp, 4 April 1984. This species was considered quite uncommon by Russell (1964) and the above records represent the only individuals which we positively identified during our fieldwork (we collected and saw large numbers of Ivory-billed Woodcreepers, *Xiphorhynchus flavigaster*). Our experience echoed that of the RAFOS who found very few Streak-headed but large numbers of Ivory-billed Woodcreepers. In contrast, the Streak-headed Woodcreeper is recorded as frequently on both Christmas Counts as the Ivory-billed (Young, 1973–1985). Since distinguishing these two species in the field is difficult, requiring cautious identification, we consider the Streak-headed to be much less common than the Ivory-billed, Christmas Count data notwithstanding.

ANTBIRDS—FORMICARIIDAE

Great Antshrike, *Taraba major*

Three mist-netted along the Sibun River near Milepost 36 of the Western Highway, 22 February 1983 by the Manomet group; male collected (CM-A3842) by the Sibun River just east of the Hummingbird Highway bridge, 20 March 1984; two males collected (CM-S8732: testes  $2 \times 1$  mm; CM-A3986) of four birds seen at CM Columbia Forest Camp, 23–26 March 1984; female collected (CM-S8909: ovary  $5 \times 3$  mm) at Big Fall, Toledo District, 1 April 1984. Russell (1964) listed only two records for the country. Young (1973–1985) recorded the species on three separate Christmas Counts. The ABWS recorded one in the

Columbia Forest Region. Great Antshrikes appear to be very local and confined primarily to the southern half of Belize.

TYRANT FLYCATCHERS——TYRANNIDAE

TYRANNULETS, ELAENIAS AND ALLIES——ELAENIINAE

Ochre-bellied Flycatcher, *Mionectes oleagineus*

In contrast to Russell's (1964) comments ("widely distributed . . . but not common or at least not seen regularly") we found this species to be the most common flycatcher in the southern forests of Belize (we encountered as many as ten individuals in one day in the Columbia Forest as opposed to a maximum of eight for any other flycatcher).

Sepia-capped Flycatcher, *Leptopogon amaurocephalus*

One collected (CM-A3863) at CM Columbia Forest Camp, 22 March 1984; one seen at CM Bladen Camp, 5 April 1984; two collected (CM-A4945; female, CM-S10125: ovary  $4 \times 5$  mm) just south of Guacamallo Bridge, 23, 24 June 1985. An uncommon species (Russell, 1964), it probably occurs throughout the southern forests. The RAFOS recorded this flycatcher three times in the Columbia Forest area.

FLUVICOLINE FLYCATCHERS——FLUVICOLINAE

Ruddy-tailed Flycatcher, *Terenotriccus erythrurus*

Two banded at Columbia Forest Station, 13 December 1971 (E. J. Fisk et al.); four collected (CM-A3883; CM-A3926; CM-A4014; female, CM-S8795: ovary  $4 \times 3$  mm) at CM Columbia Forest Camp, 22–27 March 1984; two seen at CM Bladen Camp, 3 April 1984 and one seen (same bird?) the next day. Russell (1964) listed very few records for Belize, mostly from the Columbia Forest area.

Acadian Flycatcher, *Empidonax virescens*

One banded along the Sibun River southeast of Milepost 35 of the Western Highway, 20 March 1984 (Manomet group); male collected (CM-P162533: testes  $2 \times 1$  mm) 1 km west of Augustine, 15 April 1984, in broadleaf forest. Russell (1964) listed few records and none from the western part of the country.

"Traill's" Flycatcher, *Empidonax alnorum* or *E. traillii*

The first record of either species for Belize was an individual captured on 8 October 1971 in Barclay's Bank, Belize City, by James Waite and subsequently released. This bird had been banded by Leberman at The Carnegie Museum's Powdermill Nature Reserve, 4 km S of Rector, Pennsylvania on 12 September 1971. Unfortunately, these two species are only safely separable by voice so we cannot make positive identification. We know of no subsequent records of either species from Belize.

White-throated Flycatcher, *Empidonax albigularis*

Female collected (CM-P144852) at Columbia Forest Station, 9 December 1971; one mist-netted at Columbia Forest Station, 23 March 1972, by E. J. Fisk, RCL and others. This species is not listed for Belize by Russell (1964); the specimen is the first (and only) for the country. Young (1973–1985) lists one record on the 1979 Belmopan Christmas Count.

Vermilion Flycatcher, *Pyrocephalus rubinus*

A pair seen copulating near Milepost 35 of the Western Highway, 29 June 1985. This is a rather late date for such activity, judging by Russell's (1964) data, and may represent a second nesting.

TYRANNINE FLYCATCHERS—TYRANNINAE

Rufous Mourner, *Rhytipterna holerythra*

One seen or collected each day (CM-A3963; CM-A4000) at CM Columbia Forest Camp, 25–27 March 1984; three collected (CM-A4216; CM-A4240; female, CM-S8954; ovary  $11 \times 6$  mm) at CM Bladen Camp, 4–6 April 1984; one collected of four seen (male, CM-S10092; testes  $10 \times 4$  mm) at CM Chiquibul Camp, 21 June 1985. This species was listed by Russell (1964) from few localities. Both the RAFOS and ABWS found a few individuals in the Columbia Forest area. Young (1973–1985) recorded the species only twice on the Christmas Counts.

Great Crested Flycatcher, *Myiarchus crinitus*

Male collected (CM-P162539; testes  $3 \times 1.5$  mm) 1.5 km north of Augustine, 17 April 1984. Russell (1964) considered this species to be a rare migrant. The present record is the latest spring date for the species in Belize.

Streaked Flycatcher, *Myiodynastes maculatus*

One collected of three seen (CM-A4452) at Chaa Creek, 20–21 April 1984; two collected of ten seen (CM-A4927; male, CM-S10073; testes  $12 \times 7$  mm) at CM Chiquibul Camp, 20 June 1985; male collected of two individuals seen (CM-S10232; testes  $12 \times 7$ ,  $10 \times 6$  mm) near Chan Laguna, 29 June 1985. The only other published localities for this species are Gallon Jug and Ballerina Camp (Russell, 1964). This species seems to be much more common at the western edge of Belize, and in the Chiquibul it outnumbered the normally much more common Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*).

TITYRAS AND BECARDS—TITYRINAE

White-winged Becard, *Pachyramphus polychopterus*

Male collected by Dora Weyer and John Dunning (CM-P144861) at Columbia Forest Station, 26 April 1970; female collected by Robert Askins (CM-P144862) at Columbia Forest Station, 21 August 1971; one banded at Columbia Forest Station, 10 December 1971 by E. J. Fisk et al.; male collected (CM-S8852; testes  $2.5 \times 1.5$  mm) at Big Fall, Toledo District, 29 March 1984; one captured, photographed, and released at CM Bladen Camp, 6 April 1984. These constitute the only records known to us of this species for the country.

Gray-collared Becard, *Pachyramphus major*

One mist-netted near Milepost 31 of the Western Highway, 28 February 1983 by the Manomet group. Russell (1964) listed only three records for this species: two from the far south and one from Middlesex. One individual was recorded on the 1977 Belmopan Christmas Count (Young, 1973–1985).

Rose-throated Becard, *Pachyramphus aglaiae*

One mist-netted along the Hummingbird Highway just south of Belmopan, 24 February 1983 by the Manomet group; two collected (female, CM-P166066; ovary



7 × 4 mm, brood patch; male, CM-P166071: testes 11 × 6 mm) near Chan Laguna, 29, 30 June 1985; male collected (CM-P166069: testes 10 × 4.5 mm) 6 km south and 6 km west of Progreso, 30 June 1985. Russell (1964) listed eight specimens and considered the species uncommon. Barlow et al. (1969) reported an additional two specimens from Rockstone Pond but the Royal Ontario Museum has obtained several more specimens since then (Ross James, personal communication). Rose-throated Becards have been recorded on all but one Belize City Christmas Count and on three Belmopan Christmas Counts (Young, 1973–1985). The RAFOS also found this becard in the northeast (at Altun Ha) but, in addition, recorded individuals at Guacamallo Bridge and in the Columbia Forest area. This species appears to be considerably more common in the northeastern parts of the country than elsewhere.

Black-crowned Tityra, *Tityra inquisitor*

Two collected (CM-A3874; CM-A3999) of four seen at CM Columbia Forest Camp, 22–27 March 1984; at least two seen at CM Bladen Camp, 4–6 April 1984; two seen at Chaa Creek, 16 June 1985; two collected (male, CM-S10221: testes 7.5 mm; female, CM-S10222: ovary 9 × 4 mm, largest ovum 2.5 mm) of at least four seen near Chan Laguna, 28–30 June 1985. Russell (1964) listed only a few localities where this species had been recorded. Like Russell, we found this species in close association with the Masked Tityra *T. semifasciata*.

SWALLOWS—HIRUNDINIDAE

Tree Swallow, *Tachycineta bicolor*

Ten seen in Belize City, 15 March 1984; two or three seen at Big Fall, Toledo District and at The Dump (just west of the southern terminus of the Southern Highway), 29, 30 March 1984. These are relatively late dates for this species according to Russell's (1964) data.

Bank Swallow, *Riparia riparia*

One seen at close range over the Sibun River at Hummingbird Hershey Plantation, 20 March 1984. This is the farthest inland record; most sightings are from the cays (Russell, 1964).

WRENS—TROGLODYTIDAE

White-bellied Wren, *Uropsila leucogastra*

One banded at Guanacaste Park, 9 February 1983 (Manomet group); one seen at Big Fall, 1 April 1984; encountered several times throughout western Cayo District; one captured and released at Milepost 29 of the Western Highway, 3 July 1985. Russell (1964) listed only a few localities for this species: Gallon Jug, Hill Bank, and several from western Cayo District. The RAFOS mist-netted two individuals, one in the Mountain Pine Ridge and one near Jimmy Cut. Young (1973–1985) has recorded a few individuals on Christmas Counts (both locations).

Nightingale Wren, *Microcerculus philomela*

Male collected (CM-P144854) at Columbia Forest Station, 13 December 1971 (E. J. Fisk, Leberman et al.); male collected (CM-S8763: testes 4 × 2.5 mm) CM Columbia Forest Camp, 24 March 1984. Not listed by Russell (1964). These are the first specimens for the country. Nightingale Wrens appear to be restricted to the southernmost parts of Belize.



## MUSCICAPIDS—MUSCICAPIDAE

## GNATCATCHERS—SYLVIINAE

Blue-gray Gnatcatcher, *Poliophtila caerulea*

One seen at CM Columbia Forest Camp, 22 March 1984; one seen at Big Fall, Toledo District, 1 April 1984; very common in coastal pine savannas throughout the year: five collected (two immature females, CM-P166057, 166060: almost no skull pneumatization; two adult males, CM-P166056, 166058: testes  $4 \times 3$  mm on each; adult female, CM-P166059: ovary  $4 \times 2$  mm) near Milepost 24 of the Western Highway, 26 June 1985; one collected (adult male, CM-P166076: testes  $3.5 \times 3$  mm) of four seen just north of the Belize District—Orange Walk District line along the new Northern Highway, 1 July 1985. Russell (1964) noted that this species had been seen between 28 July and 5 April but he doubted that they bred in Belize. However, he evidently did not visit the northern coastal pine savannas during May and June where these birds nest quite commonly (Weyer, personal communication). Most earlier Belizean specimens in collections have been identified as migrants of the northern subspecies *P. c. caerulea* (Russell, 1964).

## SOLITAIRES, THRUSHES AND ALLIES—TURDINAE

Brown-backed Solitaire, *Myadestes occidentalis*

One seen near the CM Chiquibul Camp, 21 June 1985. Eye-ring and contrasting back and nape color noted. This species was not listed by Russell (1964) but has been observed on a very few occasions near the western border of the country (Weyer, personal communication). Although usually considered to be restricted to high elevations (Land, 1970; Peterson and Chalif, 1973), Monroe (1968) found this species as low as 600 m (the same elevation as our sighting).

Veery, *Catharus fuscescens*

Three collected (CM-A4369; male, CM-P162534: testes  $4 \times 2.5$  mm; male [destroyed by an opossum in camp]) near the Rio Frio Cave, 16–19 April 1984. Russell (1964) listed only two records for the country, both in the fall. Young (1973–1985) recorded one bird on the 1980 Belize City Christmas Count. We think small numbers of Veeries migrate through Belize both in spring and fall but are likely to be detected only through mist-netting.

Gray-cheeked Thrush, *Catharus minimus*

Three males collected (but subsequently destroyed by an opossum in camp) near the Rio Frio Cave, 18–19 April 1984; male collected (CM-P162543: testes  $2.5 \times 1.5$  mm) at Chaa Creek, 22 April 1984. Russell (1964) lists only a few records, all from near Belize City or the cays. Young (1973–1985) recorded this species on the 1982 Belmopan Christmas Count. We think this species, like the Veery, is more common than indicated by the available records but is difficult to observe and thus usually overlooked.

Swainson's Thrush, *Catharus ustulatus*

This species was collected or seen frequently from 23 March through 23 April 1984 in all parts of the country we visited. In addition to localities mentioned by Russell (1964), we encountered these birds throughout the southern forests.

## VIREOS—VIREONIDAE

Yellow-throated Vireo, *Vireo flavifrons*

One seen in San Ignacio, 7 March 1984. Female collected (CM-S8874: ovary  $3 \times 4$  mm) near Big Fall, Toledo District, 30 March 1984. Russell (1964) noted this species as uncommon, but Young (1973–1985) has recorded this species on most Belize City Christmas Counts as well as on several Belmopan Christmas Counts.

Philadelphia Vireo, *Vireo philadelphicus*

One male collected (CM-P162538: testes 1 mm) of two birds seen near Augustine, 16 April 1984. Russell (1964) lists only one record from Belize, and Young (1973–1985) recorded one on the 1984 Belmopan Christmas Count.

Green Shrike-Vireo, *Vireolanus pulchellus*

Female collected (CM-S10103: ovary  $7 \times 5$  mm, largest ovum 2 mm) of at least five heard or seen at our CM Chiquibul Camp, 21 June 1985. Russell (1964) considered this species to be characteristic of the tall forests but not generally common in Belize. Young (1973–1985) has recorded one or two individuals on four of the last five Belmopan Christmas Counts. We found it only in the Chiquibul but it appeared to be common there.

Rufous-browed Peppershrike, *Cyclarhis gujanensis*

One seen at the edge of high hardwood forest just northeast of Columbia Forest Station, 14 December 1971 (Leberman); two collected (female in breeding condition: CM-P166077, ovary  $10 \times 5$  mm; bird of unknown sex: CM-A5010) of at least four birds seen between Milepost 24 and 29 of the Western Highway, 1–4 July 1985. In the Yucatan Peninsula, this species inhabits treetops in thin deciduous forest (Paynter, 1955; Parkes, personal communication), but Russell (1964) noted that in Belize these birds are restricted to dense undergrowth in lowland pine forests (and perhaps in mangrove swamps). While this species may be most common in the lowland pine forests, our experience indicates that they are not restricted to this habitat. Young (1973–1985) has recorded from one to five individuals on each of the last six Belize City Christmas Counts.

## EMBERIZIDS—EMBERIZIDAE

## WOOD WARBLERS—PARULINAE

Blue-winged Warbler, *Vermivora pinus*

Individuals either seen or collected at each of the locations we visited during March and April 1984 except Chaa Creek. A banded individual collected at the CM Bladen Camp is reported elsewhere (Wood and Adams, 1985). We consider the species to be more common than suggested by Russell (1964; 26 scattered records). Young (1973–1985) listed one to seven individuals on every Christmas Count except one.

Golden-winged Warbler, *Vermivora chrysoptera*

One seen near Rio Frio Cave, 14 April 1984. Russell (1964) listed only five records for Belize and Young (1973–1985) recorded one individual each on the 1979 and 1982 Belmopan Christmas Counts.

Tennessee Warbler, *Vermivora peregrina*

One or two seen each day at CM Columbia Forest Camp 23–27 March 1984; four collected (CM-A4068, 4092, 4106, 4137) of at least 12 seen at Big Fall, Toledo District, 29 March–1 April 1984; other individuals seen elsewhere in the country. Contrary to Russell (1964) we consider this species to be a common transient in Belize, at least in the forested sections.

Cape May Warbler, *Dendroica tigrina*

One seen near Punta Gorda, 4 December 1971 (Leberman and K. S. Anderson); one seen along Hummingbird Highway near the Sibun River, 24 February 1983 (Manomet group, Leberman); one seen on Coco Plum Cay, 11 March 1984. Russell (1964) lists only two records. Young (1973–1985) recorded two on the 1974 Belize City Christmas Count. However, this species is probably not as rare as the limited number of sightings suggests (Weyer, personal communication).

Black-throated Blue Warbler, *Dendroica caerulescens*

One seen at CM Columbia Forest Camp, 22 March 1984, the first published record from the southern parts of Belize. Young (1973–1985) recorded individuals of this species on three Christmas Counts.

Cerulean Warbler, *Dendroica cerulea*

Male collected (CM-P162530; testes  $5 \times 3$  mm) near Rio Frio Cave, 14 April 1984. Russell (1964) listed very few records for this rare transient and none from Cayo District. Young (1973–1985) recorded the species on the 1978 and 1984 Belize City Christmas Counts.

Swainson's Warbler, *Limnothlypis swainsonii*

One banded at Columbia Forest Station, 28 March 1972 (E. J. Fisk et al.); one banded along Sibun River southeast of Milepost 35 on the Western Highway, 4 February 1983 (Manomet group); six banded at Guanacaste Park, one each on 7 and 8 February 1983, two each on 23 and 24 March 1984 (Manomet group); two collected (CM-A3824, 3831) at Altun Ha, 18, 19 March 1984. Russell (1964) listed only four records for this rare warbler. The only other published records from Belize is of two seen on the first Belize City Christmas Count (Young, 1974–1985) and of one seen on Cay Chapel by the ABWS.

Ovenbird, *Seiurus aurocapillus*

We found this species to be one of the most abundant birds in the southern forests during our March 1984 visit; up to ten individuals were observed each day. Russell (1964) listed it as a moderately common transient and winter resident.

Louisiana Waterthrush, *Seiurus motacilla*

Several seen at Columbia Forest Station in December 1971 and March 1972 (E. J. Fisk et al.); one collected (CM-A4166) of two seen at the CM Bladen Camp, 3, 5 April 1984; female collected (CM-P162541, ovary  $6 \times 2.5$  mm) near Rio Frio Cave, 16 April 1984. Russell (1964) listed very few records but we think this species is more common than he suggested. Young (1973–1985) recorded the species on six Christmas Counts and both the RAFOS and ABWS reported individuals from the Columbia Forest area.

Gray-throated Chat, *Granatellus sallaei*

Female collected (CM-P144869, ovary not enlarged) at Columbia Forest Station, 24 March 1972 (E. J. Fisk et al.); male captured, photographed, and released at Chaa Creek, 16 June 1985. The Columbia Forest Station specimen is the first record from Toledo District. Only two locations (Gallon Jug and Cayo) are listed for this rare resident by Russell (1964).

## BANANAQUITS—COEREBINAE

Bananaquit, *Coereba flaveola*

Three seen at close range in Guanacaste Park, 6 March 1984; one seen at Dangriga, 21 March 1984; two collected (CM-S8824, female, ovary  $5 \times 4$  mm; CM-S8825, male, testes  $7 \times 4$  mm) at Big Fall, Toledo District, 28 March 1984; one collected (CM-P162510, male, testes  $7 \times 4.5$  mm) of six seen at Big Fall, Toledo District, 31 March 1984; two seen at CM Bladen Camp, 4 April 1984. This species was not encountered by the Louisiana State University personnel, and Russell (1964) knew of only two old records. The fact that Russell spent relatively little time in the south of Belize may account for the lack of sightings, but Bananaquit populations may also be increasing; we consider the species common in the southern forests. Both the RAFOS and ABWS encountered this species in the Columbia Forest area. Young (1973–1985) reported up to four individuals on every Belize City Christmas Count except in 1977 and also listed it on four Belmopan counts.

## TANAGERS—THRAUPINAE

Common Bush-Tanager, *Chlorospingus ophthalmicus*

One seen and carefully identified by Leberman and K. S. Anderson independently at Columbia Forest Station, 9 December 1971, is only the second record for Belize (Russell, 1964). Although this is thought to be a montane bird, some individuals apparently venture to lower elevations along the foothills of the Maya Mountains.

## CARDINALS AND ALLIES—CARDINALINAE

Blue Grosbeak, *Guiraca caerulea*

We agree with Russell's (1964) comments for this species, except we found these birds common into the early part of April (rather than late March) and recorded four at Augustine as late as 16 April 1984 and one the following day.

## EMBERIZINES—EMBERIZINAE

Olive Sparrow, *Arremonops rufivirgatus*

Five collected of many seen in open pine forest between Milepost 24 and Milepost 30 of the Western Highway, 13, 14 June 1985; at least six seen in open pine forest along the new Northern Highway at the Belize-Orange Walk District boundary. Russell (1964) apparently spent very little time in the pine forests between Belize City and Belmopan, otherwise he would have had to encounter this species which is common there. Russell's few records are from the north-eastern portion of Belize.

Grassland Yellow-Finch, *Sicalis luteola*

One collected (CM-P144865) at Mussel Creek Rice Station, 10 October 1971, the first record for Belize. Young (1973–1985) recorded a flock of 100 on the 1981

## Belize City Christmas Count and a flock of 16 on the 1984 Belize City Christmas Count.

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A REVIEW OF THE CRANE FLIES IN THE SUBGENUS  
*TIPULA (PAPUATIPULA)* (DIPTERA: TIPULIDAE),  
WITH DESCRIPTIONS OF FIVE NEW SPECIES

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ABSTRACT

The subgenus *Tipula (Papuatiptula)* is reviewed. Twenty-three species are recognized with five species from Papua New Guinea being newly described: *Tipula (Papuatiptula) insperata*, *Tipula (Papuatiptula) koiari*, *Tipula (Papuatiptula) nigritus*, *Tipula (Papuatiptula) oneili*, and *Tipula (Papuatiptula) wibleae*. A key is provided to identify all species for which types have been examined. Female brachyptery and gynandromorphy in *Tipula (Papuatiptula) koiari*, n. sp., are discussed.

INTRODUCTION

The subgenus *Papuatiptula* (Alexander, 1935) of the large and extensive genus *Tipula* (Linnaeus, 1758) contains a small group of species from New Guinea. This review was stimulated by the discovery of five new taxa collected during a recent field trip to Papua New Guinea. It is an effort to clarify the systematic limits of this subgenus, and to investigate its relationship to other subgenera within *Tipula*.

Species of *Papuatiptula* are poorly represented in collections, and specimens other than type materials are lacking for comparative study. Many of the older types are in poor condition, having been improperly mounted or subsequently mishandled. Species of subgenus *Papuatiptula* are the most frequently encountered and the most diverse species of *Tipula* in New Guinea. Many more species will undoubtedly be found when the fauna is better collected, therefore, a revision of the subgenus at this time would be premature. The following review is primarily a redefinition of the subgenus, a key and descriptions of five new species, and should provide a foundation for future systematic and biological studies.

TAXONOMIC HISTORY

The subgenus *Papuatiptula* was first proposed by C. P. Alexander (1935:52), who described it as follows:

"... Antennae 13-segmented; flagellar segments with verticils that greatly exceed the segment in length. Tibial spurs long and conspicuous; formula 1-2-2. Wings with Rs unusually short but not transverse, ... squama naked ..."

The subgenus was described in *Tipula* and the five originally included species were *Tipula (Papuatiptula) divergens* de Meijere, *T. (P.) leucosticta* Alexander, *T. (P.) meijereana* Alexander, *T. (P.) novaebritanniae* Alexander, and *T. (P.) omis-sinervis* (de Meijere). *T. (P.) novaebritanniae* was designated as the type species. Alexander subsequently described an additional thirteen species (Oosterbroek and Jonas, 1986): *T. (P.) artifex* Alexander, *T. (P.) consiliosa* Alexander, *T. (P.) gres-*

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*sittiana* Alexander, *T. (P.) lieftincki* Alexander, *T. (P.) melanotis* Alexander, *T. (P.) nokicola* Alexander, *T. (P.) obediens* Alexander, *T. (P.) pensilis* Alexander, *T. (P.) satirica* Alexander, *T. (P.) staryi* Alexander, *T. (P.) strictistyla* Alexander, *T. (P.) surcularia* Alexander, and *T. (P.) toxopeina* Alexander. He transferred two other species, *T. (P.) cyclopica* Alexander and *T. (P.) pedicioides* Alexander from the subgenus *Acutipula* (Alexander) to *Papuatipula* (Alexander, 1973). Twelve holotypes and four paratypes of the twenty described species have been examined and compared to the study materials consisting of 71 specimens in The Carnegie Museum of Natural History (CMNH) and 5 specimens from the Bernice P. Bishop Museum.

When first established, the subgenus was characterized by venation, naked squamae, and the male hypopygia. Some of these characters are no longer diagnostic for *Papuatipula* because of variation among the species that were subsequently transferred to the subgenus. Moreover, when the holotype of *T. novae-britanniae* was examined, the squamae were not naked but bore a cluster of eight setae, despite Alexander's original description. The present study has demonstrated that venational differences, such as the length of vein Rs compares to m-cu, vary among the species and are of little value in delimiting the group. The structures of the male hypopygium, on the other hand were found to be the most informative taxonomic features and have been used to characterize this subgenus. With the addition of the five new species described below and the removal of *T. nokicola* and *T. pedicioides*, 23 species of *Papuatipula* are recognized at this time.

#### SYSTEMATICS

##### Family Tipulidae Subgenus *Papuatipula*

**Description.**—The terminology used in this section, in the following key to species, and in the species descriptions, follows Byers (1961) and McAlpine (1981).

**Head:** Rostrum well developed, 1.5 to twice length of rest of head, nasus distinct. Frons moderately broad with medial tubercle. Antenna 13-segmented, subequal to length of head; two short and three long verticillate setae arise from base of each flagellomere. Terminal segment of maxillary palp flagelliform, longer than four preceding segments together.

**Thorax:** Wing clear with dark brown stigma and paler brown quadrate area before middle of cell CuA, or striped with longitudinal brown and white pattern with a white band before cord and dark pigment narrowly present along veins CuA, m-cu, and r-m. Squama setose. Tibial spur formula 1-2-2. Male claws with two teeth; female claws simple or with single tooth.

**Abdomen:** Abdomen slender, in male slightly shorter than wings, in female usually longer.

**Hypopygium:** Tergite 9 separates from sternite 9; basistyle fused with sternite; sternite 8 unarmed. Tergite 9 notched medially bearing small spines. Outer dististyle lobed, cylindrical, pigmented apically. Inner dististyle variable.

**Ovipositor:** Tergite 9 short, not produced laterally. Cerci long and extreme slender, smooth-margined, fused to tergite 10; hypovalves shorter than cerci and fused basally. Valvulae fused at base, slightly sclerotized posteriorly.

**Diagnosis.**—The subgenus can be separated morphologically from other subgenera of *Tipula* by the following characters: squamae setose, tibial spur formula 1-2-2, male hypopygium with ninth tergite and sternite separated and ninth tergite notched medially, and the outer dististyle sclerotized. The last two characters appear to be apomorphic thus species of *Papuatipula* may form a monophyletic group.

Three other subgenera of *Tipula* are sympatric with *Papuatipula* in New Guinea (Alexander, 1961). They are *Acutipula* (Alexander), *Indotipula* (Edwards), and *Tipulodina* (Enderlein). Species of *Tipulodina* have long legs that are ringed with



snowy white on the femora, tibiae, or basitarsi. Species of *Indotipula* have naked squamae and clear, iridescent wings. The subgenus *Acutipula* was characterized primarily by having the ninth tergite and sternite fused laterally and by having unbranched weakly sclerotized outer dististyle. Species of *Papuatipula* bear a strong resemblance to those of *Acutipula*, but can be distinguished easily from the other subgenera.

*Tipula nokiicola* (Alexander, 1953) and *T. pedicioides* (Alexander, 1948) are excluded from *Papuatipula* due to several morphological characters. In *T. nokiicola*, the presence of a strongly sclerotized outer lobe at the base of the inner dististyle in the male and iridescent transparent wings suggest a relationship to sympatric *Indotipula* species. However, the presence of setae on the squamae is similar to the condition in *Papuatipula*. *T. pedicioides* was described in 1948 in the subgenus *Acutipula* and was transferred to *Papuatipula* by Alexander (1973). The relatively large, unbranched outer dististyle suggests an affiliation with *Acutipula*. More specimens and study are needed to assess the systematic position of both *T. pedicioides* and *T. nokiicola*.

*Included species.*—Characters found useful in segregating species of *Papuatipula* are as follows: (1) wing pattern; (2) shape of flagellomeres; (3) shape of the ninth tergal lobes; (4) degree of sclerotization of the outer dististyle; (5) shape of the inner dististyle; (6) length of the cerci relative to the hypovalves. The following key to species is based primarily on the most easily visible genitalic characters of males and includes only those species for which type specimens have been examined, therefore, omitting *T. divergens*, *T. leucosticta*, *T. lieftincki*, *T. meije-reana*, *T. omissinervis*, and *T. surcularia*.

#### KEY TO SPECIES OF *PAPUATIPULA*

1. Wings longitudinally striped with brown and white; dark pigment narrowly present along vein CuA ..... 2
1. Wings unmarked except for the stigmal darkening and a quadrate dark mark at middle of cell CuA ..... 15
2. Wings with dark pattern strongly contrasting, whitish crossband at cord extensive; white pattern covering about half of cells M<sub>1</sub>, 2nd M<sub>2</sub> and M<sub>3</sub> ..... 3
2. Wings with dark pattern diffuse, not strongly contrasting, no whitish crossband at cord; white pattern less extensive, only covering bases of cells M<sub>1</sub> and 2nd M<sub>2</sub> ..... 7
3. Size large, wing length over 30 mm ..... *T. wibleae*, new species
3. Size smaller, wing length under 25 mm ..... 4
4. Cell CuA<sub>1</sub> entirely dark ..... *T. koirai*, new species
4. Cell CuA<sub>1</sub> entirely clear or with more than apical half clear ..... 5
5. Proximal half of outer dististyle dilated ..... *T. toxopeina*
5. Outer dististyle simple, not dilated ..... 6
6. Ninth tergite of male shallowly emarginated ..... *T. gressittiana*
6. Ninth tergite of male broadly emarginated forming V-shaped notch ..... *T. staryi*
7. Ninth tergite of male with two medial lobes and two lateral lobes ..... 8
7. Ninth tergite of male without lateral lobes ..... 10
8. Medial lobes on ninth tergite of male separated by a deep U-shaped notch ..... *T. nigrinus*, new species
8. Medial lobes nearly approximate at base ..... 9
9. Outer dististyle strongly sclerotized with two large teeth on mesal margin ..... *T. insperata*, new species
9. Outer dististyle with one tooth on mesal margin ..... *T. artifex*
10. Medial lobes on ninth tergite of male separated by very narrow notch ..... 11
10. Medial lobes on ninth tergite of male separated by broad U-shaped notch ..... 14
11. Outer dististyle deep bifid ..... *T. satirica*
11. Outer dististyle simple ..... 12
12. Outer dististyle with two large apical teeth ..... *T. pensilis*

12. Outer dististyle with single dark point ..... 13
13. Inner dististyle with beak broadly compressed ..... *T. strictistyla*
13. Inner dististyle with beak long and slender ..... *T. consiliosa*
14. Outer dististyle long, straight, rod-shaped, with sharp apical spine ..... *T. melanotis*
14. Outer dististyle broad, compressed ..... *T. cyclopica*
15. Outer dististyle rod-shaped, apex bifurcate with dark serrate spur extending inward .....  
..... *T. oneili*, new species
15. Outer dististyle broad, compressed ..... 16
16. Outer dististyle bifurcate, one edge with a sharp spine, the other with a group of spinuloid  
setae ..... *T. obediens*
16. Outer dististyle simple, with one apical spine ..... *T. novaebritanniae*

***Tipula (Papuatiptula) insperata* Young, new species**

(Fig. 1-3)

*Description.*—Body length: Male, 16 mm; female, 22 mm. Wing length: Male, 21 mm; female, 23 mm.

**Head:** Occiput and rostrum brown; palpi with first three segments yellow, terminal segment brown. Frontal tubercle with median longitudinal groove. Antenna with scape, pedicel and first flagellomere yellow; flagellomeres distinctly bicolored, dark brown basally, remainder yellow; all flagellomeres except last subequal in length; five setae in verticil arising from base of each flagellomere, longest about three times length of flagellomere.

**Thorax:** Pronotum reddish brown. Scutum brown with four light brown stripes, median stripes divided anteriorly by dark brown interspace. Scutum, scutellum and mediotergite brown, pollinose. Pleura yellowish brown, pollinose, with one narrow dark brown longitudinal stripe across cervical sclerite, proepisternum, upper anepisternum, and base of wing to katatergite. Legs with coxae and trochanters yellow; femora yellow with conspicuous subapical brown band; tibiae and basitarsi yellow with apices dark; remainder of tarsi brown. Wings tinged with brown; dark areas at stigma, distal side of anterior cord, postarcular region; a conspicuous dark brown quadrate spot before middle of cell CuA<sub>1</sub> preceded and followed by whitish subhyaline areas; dark pigment narrowly bordering veins CuA and base of CuA<sub>1</sub>. Halteres brown.

**Abdomen:** Ground color yellowish brown. First segment gray, tergites 2 to 4 brown with gray lateral borders, basal rings glabrous, subbasal impressions conspicuous; tergites 5 to 7 dark brown. Sternite brownish yellow.

**Hypopygium:** External structures as in Fig. 1, 2. Tergite 8 much shorter than tergite 9. Tergite 9 terminating in two very dark lobes medially, separated by a small rectangular notch; margins of lobes with spines; outer lateral angle of tergite 9 produced into lower glabrous lobe. Outer dististyle dark brown, with dark apical point posteriorly and curved inwards bearing two large teeth on mesal margin before apex. Inner dististyle with beak slender; lower beak large, dark; outer basal lobe smaller, rounded.

**Ovipositor:** External structures as in Fig. 3. Cerci slightly longer than tergite 10. Hypoalves extending to about one-third length of cerci.

*Type material.*—Holotype: Male, Papua New Guinea, Northern Province, Myola (147°44'E, 9°9'S), Iora Creek, 4 June 1984, Chen W. Young. Paratype: One female, topotypic. Types are in the collection of the CMNH.

*Etymology.*—The name *insperata* (Latin, unexpected) was selected because of the unexpected capture of a mating pair along the bank of Iora Creek.

***Tipula (Papuatiptula) koiari* Young, new species**

(Fig. 4-7)

*Description.*—Body length: Males, 17-18 mm; females, 19-20 mm. Wing length: Males, 20-21 mm; females, 9-10 mm.

**Head:** Occiput and rostrum pale brown, pollinose; palpi dark brown. Frontal tubercle with median longitudinal groove. Antenna with scape and pedicel yellow; flagellomeres faintly bicolored, brownish black basally, remainder brown; all flagellomeres except last subequal; five verticillate setae arising from base of each flagellomere, longest subequal in length to flagellomere.

**Thorax:** Pronotum grayish brown. Scutum with two dark brown longitudinal median stripes and two short indistinct lateral stripes. Pleura pale brown except laterotergites darker. Legs with coxae and trochanters yellowish brown slightly tinged with gray; remainder of legs brown, gradually darker

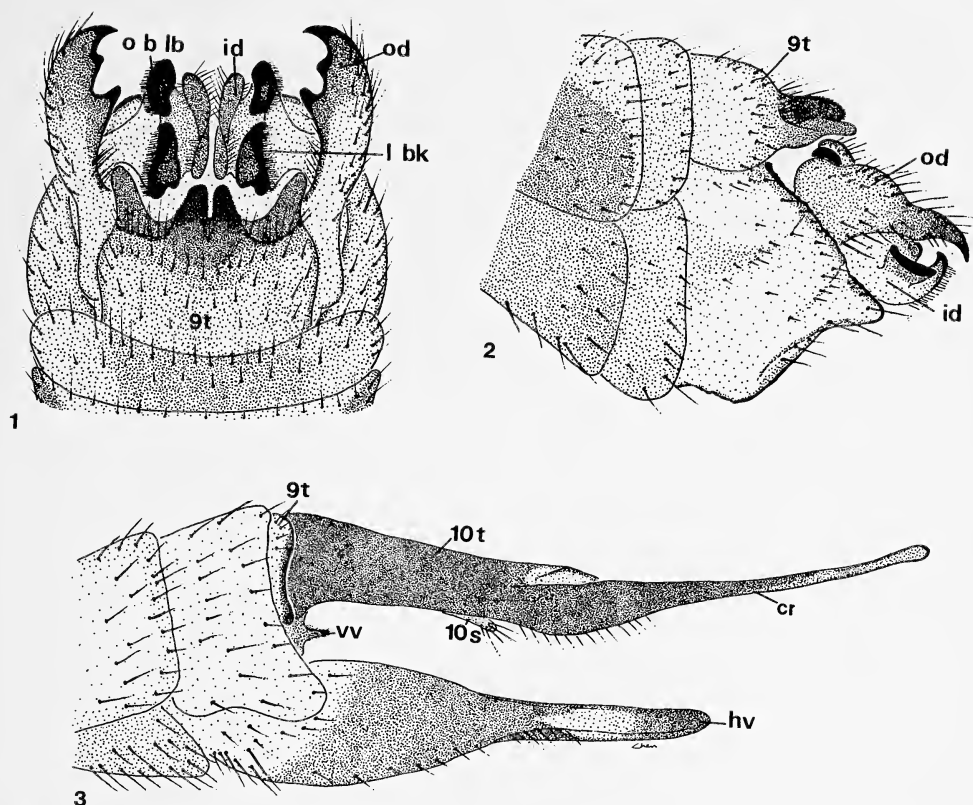


Fig. 1, 2.—*Tipula* (*Papuatiptula*) *insperata* male hypopygium. 1. Dorsal view. 2. Lateral view. 9t—ninth tergite, id—inner dististyle, 1 bk—lower beak of inner dististyle, o b lb—outer basal lobe of inner dististyle, od—outer dististyle. Fig. 3.—*T. (P.) insperata* female ovipositor lateral view. 9t—ninth tergite, 10s—tenth sternite, 10t—tenth tergite, cr—cercus, hv—hypo valve, vv—valvulae.

distally; apices of femora and tibiae dark. Wings tinged with grayish brown, darker along costal margin, on veins CuA, base of CuA<sub>1</sub>; dark brown clouding at stigma and middle of cell CuA. Clear areas in cell 1st M<sub>2</sub>, base of cells M<sub>1</sub> and M<sub>2</sub>, and apical one-third of cell R<sub>5</sub>. Female brachypterous, wings short and narrow with all veins visible. Knobs of halteres brownish black, stems yellowish brown.

**Abdomen:** Ground color brown, pollinose; first segment yellowish brown; tergites 2 to 7 brown with brownish black lateral margins forming a stripe interrupted by distinct subbasal impressions. Sternites 1 and 2 yellowish brown, other sternites gradually darker posteriorly. Female abdomen unusually large.

**Hypopygium:** External structures as Fig. 4, 5. Tergite 8 short, broadly emarginate; tergite 9 rounded at sides, with two median lobes distally, separated by shallow notch; apex of lobes with dense, black spines. Outer dististyle large, pale brown, curved inward with one large pre-apical tooth about mid-length; distal edge of outer dististyle heavily pigmented, serrate, with rounded apical tip. Inner dististyle with beak broad, directed anteriorly; lower beak lobed, dark; outer basal lobe small with dark outer margin.

**Ovipositor:** External structures as Fig. 6. Cerci slightly longer than tergite 10, narrowed at base, tapered posteriorly; sternite 10 pale, bearing setae at posterior margin. Hypo valves extending to about half length of cerci.

**Type material.**—Holotype: Male, Papua New Guinea, Northern Province, Myola, 2 June 1984, James A. Bossert, John W. Ismay, Chen W. Young. Paratypes: Thirty-two males, thirteen females, topotypic. The holotype and several paratypes

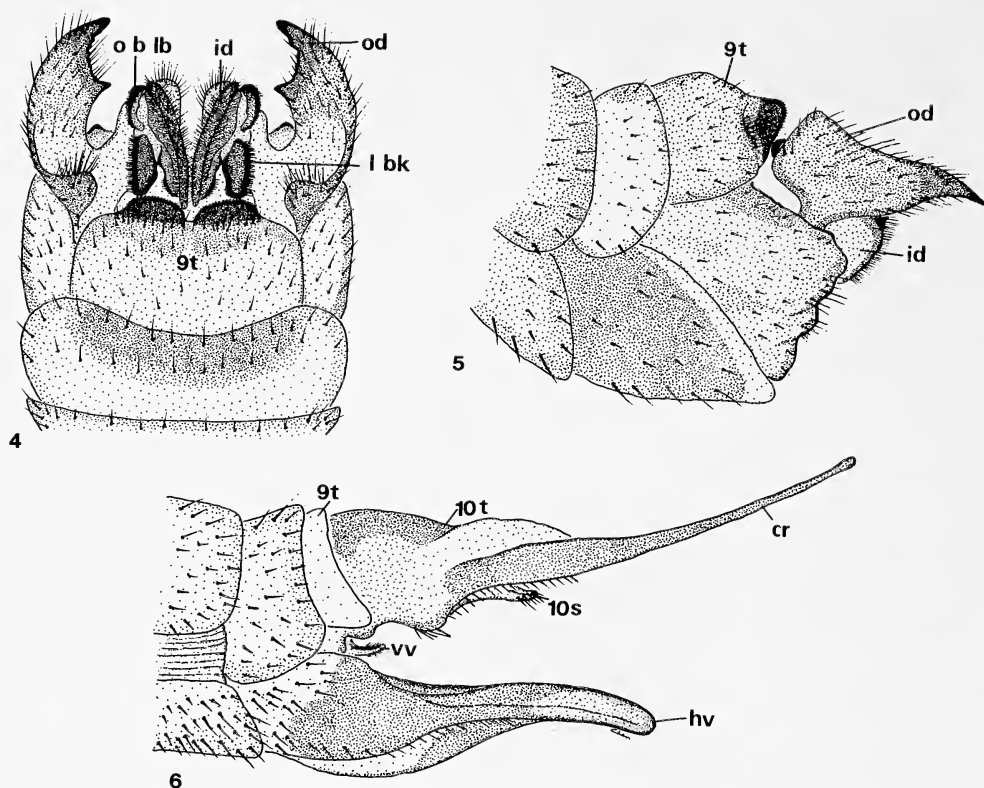


Fig. 4, 5.—*Tipula (Papuatipula) koiari* male hypopygium. 4. Dorsal view. 5. Lateral view. 9t—ninth tergite, id—inner dististyle, l bk—lower beak of inner dististyle, o b lb—outer basal lobe of inner dististyle, od—outer dististyle. Fig. 6.—*T. (P.) koiari* female ovipositor lateral view. 9t—ninth tergite, 10s—tenth sternite, 10t—tenth tergite, cr—cercus, hv—hypovalve, vv—valvulae.

are deposited in CMNH. One male paratype is deposited in each of the following institutions: Central Reference Insect Collection, Konedobu, Papua New Guinea; Bernice P. Bishop Museum, Honolulu, Hawaii; National Biological Institute, Bogor, Indonesia; Institute of Taxonomic Zoology, University of Amsterdam, Netherlands; Snow Entomological Museum, University of Kansas, Lawrence, Kansas; United States National Museum of Natural History, Washington, D.C.; British Museum (Natural History), London, England.

*Etymology.*—This species is named after the Koiari tribesmen on whose land the type series was collected.

*Remarks.*—The type series of this species was collected in a montane meadow. The habitat was a saturated marsh dominated by *Juncus*. This homogeneous habitat at high altitude (2200 m), coupled with low temperatures and frequent windy conditions, probably explains the occurrence of female brachyptery (Byers, 1969). Mating pairs were observed at night. Copulating females grasped blades and culms of grass with their front legs, while copulating males hung freely upside-down by their genitalia.

A gynandromorphic specimen (Fig. 7) was collected on 4 June 1984. This specimen has a well developed left wing, which is only slightly shorter than the

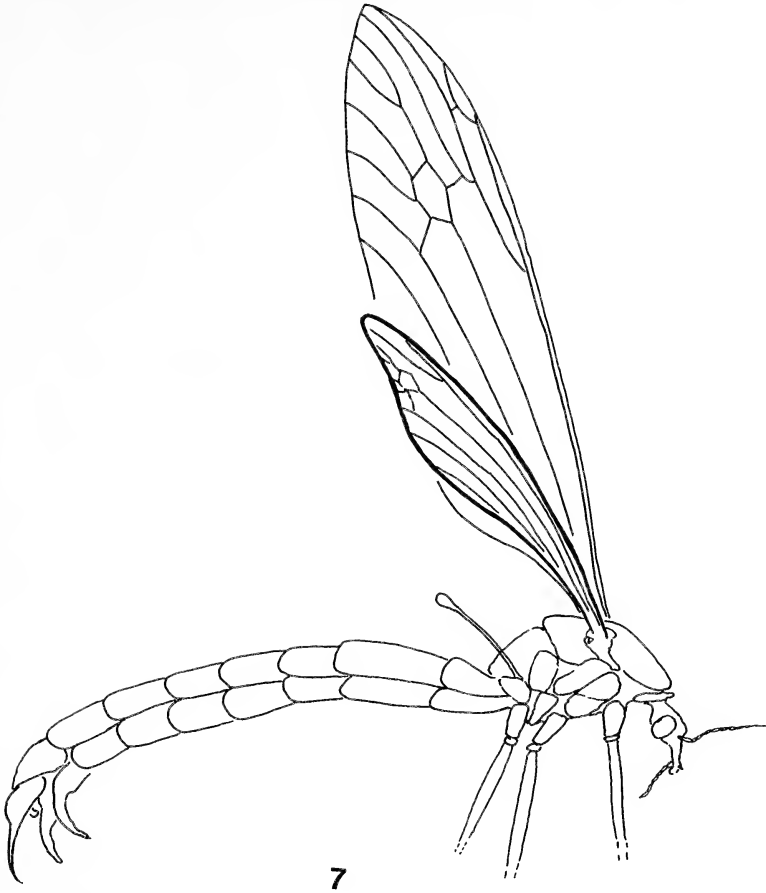


Fig. 7.—*Tipula* (*Papatipula*) *koiari*. A gynandromorphic specimen showing brachypterous female form with a well developed left wing and a vaguely defined male hypopygium.

wing of a male. The right wing has the brachypterous female form. The abdomen terminates in an ovipositor. One cercus is present on the right side, and the left side is a vaguely defined male hypopygium. Both hypovalves are present on the ventral side. This specimen is in the collection of the CMNH.

***Tipula* (*Papatipula*) *nigritus* Young, new species**  
(Fig. 8–10)

**Description.**—Body length: Males, 16–17 mm; female, 23 mm. Wing length: Males, 18–19 mm; female, 21 mm.

**Head:** Occiput and rostrum dark brown; palpi dark brown. Frontal tubercle with median longitudinal groove. Antenna with scape and pedicel dark brown, flagellomeres beyond first vaguely bicolored, dark brown basally, remainder brown; flagellomeres subequal in length becoming shorter distally; five verticillate setae arising from base of each flagellomere, longest subequal in length to flagellomere.

**Thorax:** Pronotum dark brown. Scutum reddish brown with four longitudinal stripes bordered by dark brown, interspaces grayish brown; median stripes confluent anteriorly, and with pale median line posteriorly. Scutum, scutellum and mediotergite brown, pollinose. Pleura dark brown, pollinose. Legs dark brown, apices of femora and tibiae slightly darker. Wings patterned with pale brown and white;

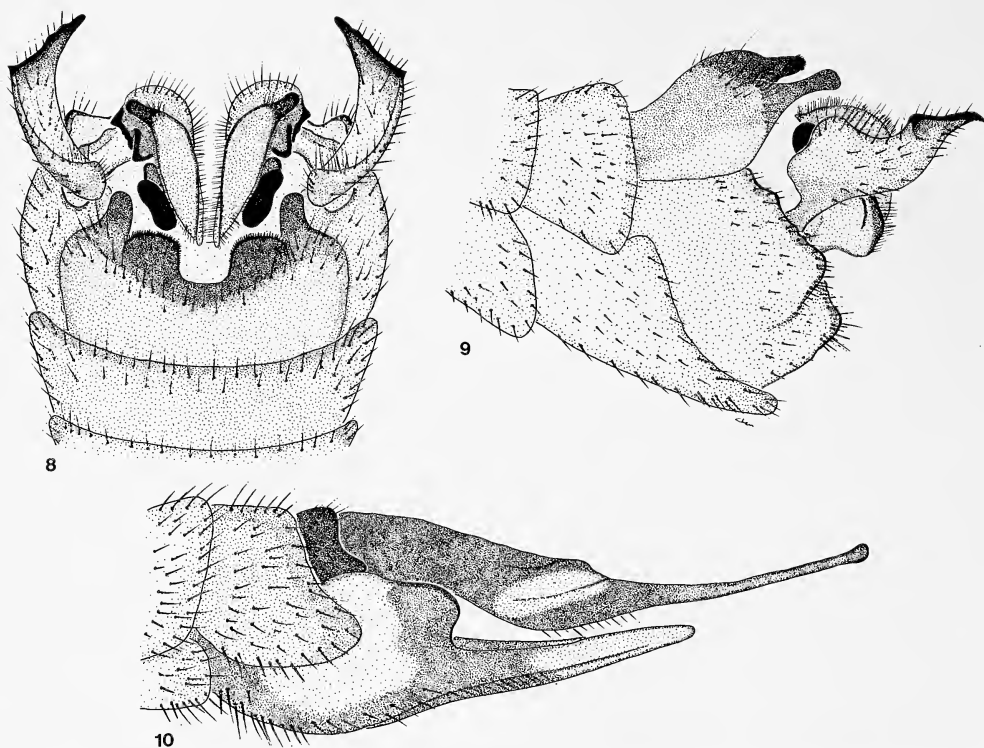


Fig. 8, 9.—*Tipula (Papuatiptula) nigrilus* male hypopygium. 8. Dorsal view. 9. Lateral view. Fig. 10.—*T. (P.) nigrilus* female ovipositor lateral view.

dark areas include stigma, prearcular region, base of cell  $R_{4+5}$ , base of cell  $CuA_1$ , and middle of cell  $CuA$ . Halteres dark brown.

**Abdomen:** Ground color brown with terga darker than sterna. Tergites 2 to 4 with pale basal rings and subbasal impressions.

**Hypopygium:** External structures as Fig. 8, 9. Tergite 8 short; tergite 9 terminating in two broadly rounded dark mesal lobes and two outer, lower lobes, mesal lobes widely separated by U-shaped notch, margins of mesal lobes with spines. Outer dististyle narrow at base, broad at middle; apex obliquely truncate with dark edge. Inner dististyle with beak broad, compressed; lower beak a small dark lobe; outer basal lobe bifurcate with dark margin.

**Ovipositor:** External structures as Fig. 10. Cerci slightly longer than tergite 10, with round apical expansion. Hypovalues extending to about one-third length of cerci, with basal lobe broad laterally.

**Type material.**—Holotype: Male, Papua New Guinea, Morobe Province, Wau Ecological Institute, 28 December 1965, J. & M. Sedlacek. Paratypes: Three males and one female, topotypic. Holotype, 1 male paratype, and 1 female paratype are in the collection of the Bernice P. Bishop Museum, Honolulu, Hawaii. Two male paratypes are deposited in the CMNH.

**Etymology.**—The name *nigrilus* emphasizes the relatively dark pigmentation of this species.

***Tipula (Papuatiptula) oneili* Young, new species**  
(Fig. 11–13)

**Description.**—Body length: Males, 18–20 mm; females, 28–30 mm. Wing length: Males, 23–25 mm; females, 24–25 mm.

**Head:** Occiput and rostrum brown; palpi with first segment yellowish brown, remainder dark. Frontal

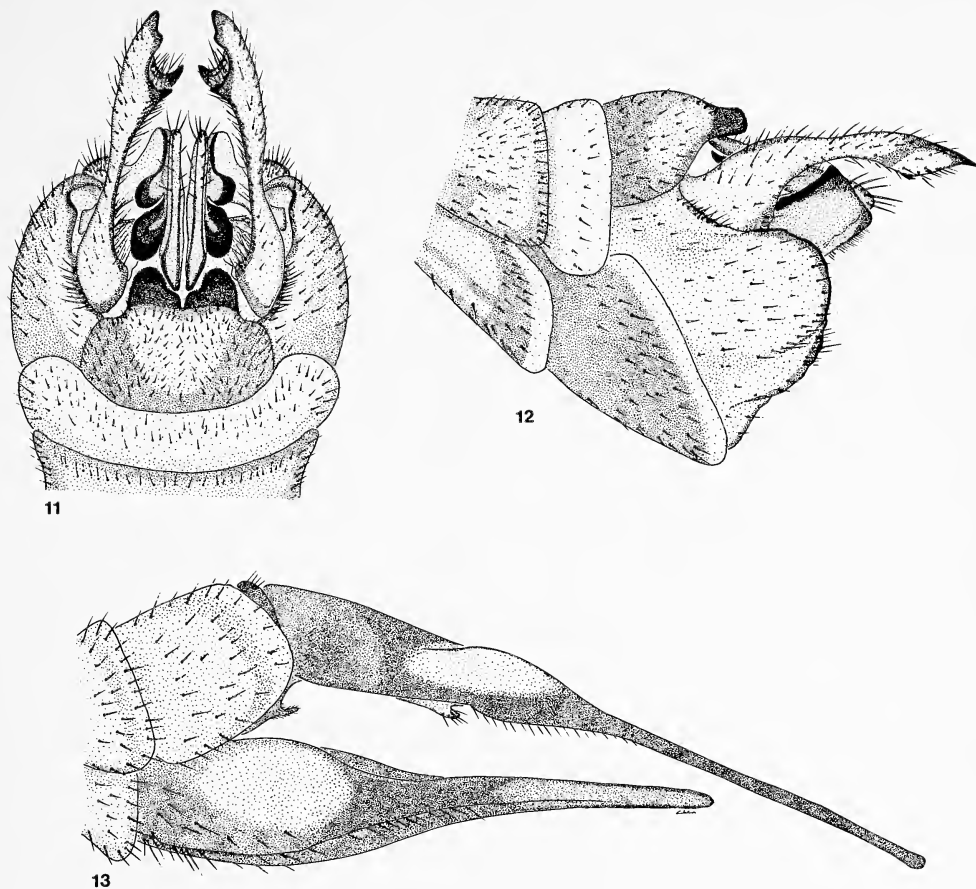


Fig. 11, 12.—*Tipula* (*Papatipula*) *oneili* male hypopygium. 11. Dorsal view. 12. Lateral view. Fig. 13.—*T. (P.) oneili* female ovipositor lateral view.

tubercle with median longitudinal groove. Antenna with scape and pedicel yellow, flagellomeres 2 to 8 bicolored, brown basally with remainder yellowish brown; all except apical flagellomeres subequal in length; five verticillate setae arising from base of each flagellomere, longest about twice length of flagellomere.

**Thorax:** Pronotum gray. Scutum brown with four slightly darker brownish gray stripes bordered narrowly with brown. Scutum, scutellum, mediotergite, and pleura evenly gray, pollinose. Legs with coxae and trochanters gray; femora and tibiae yellow, apices dark brown; tarsi light brown, gradually darker toward apices. Wings grayish subhyaline, with darker area at stigma and faint pattern of brown before middle of cell CuA toward base. Halteres grayish brown.

**Abdomen:** First segment gray; tergites 2 to 4 yellowish brown; tergites 5 to 8 dark brown. Sternites dark brown.

**Hypopygium:** External structures as in Fig. 11, 12. Tergite 8 short; tergite 9 with two low, slightly obtuse lobes separated by a narrow notch posteriorly, lobes emarginate medially, edged with spines. Outer dististyle long, broad at base, narrowed near mid-length, expanded apically; apex bifurcate with a dark flange extending mesad. Inner dististyle with beak slender; lower beak a dark lobe; outer basal lobe smaller than lower beak with dark margin.

**Ovipositor:** External structures as Fig. 13. Cerci long, about twice length of tergite 10. Hypoalves broad basally, tapered posteriorly, extending to about half length of cerci.

**Type material.**—Holotype: Male, Papua New Guinea, Morobe Province, Wau Ecological Institute, 13 May 1984, Chen W. Young. Paratypes: Two males and



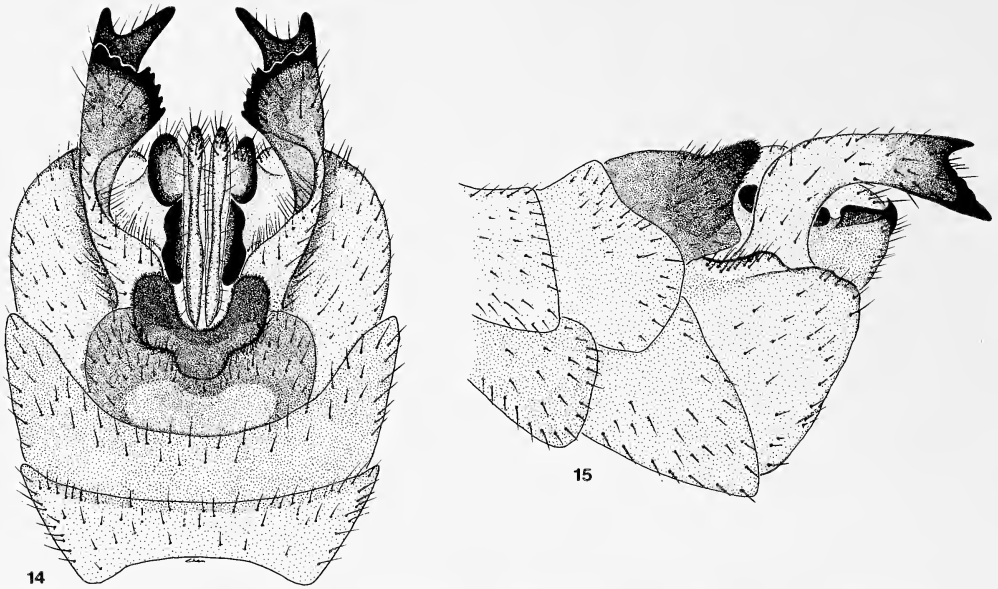


Fig. 14, 15. *Tipula (Papuatipula) wibleae* male hypopygium. 14. Dorsal view. 15. Lateral view.

two females topotypic; two males, two females, Northern Province, near Tufi, 10 September 1982, John W. Ismay. Holotype and four paratypes are in the collection of the CMNH. Other paratypes are deposited in Central Reference Insect Collection, Konedobu, Papua New Guinea, and the Bernice P. Bishop Museum, Honolulu, Hawaii.

**Etymology.**—This species is named in honor of Mr. Edward O'Neil for his generosity in funding the field activities of the Section of Invertebrate Zoology, CMNH.

**Remarks.**—Specimens of this species were collected from low herbaceous plants growing along the forest edge.

***Tipula (Papuatipula) wibleae* Young, new species**  
(Fig. 14, 15)

**Description.**—Body length: Males 25–27 mm; female, unknown. Wing length: Males, 32–35 mm.

**Head:** Occiput and rostrum yellowish brown; palpi dark brown. Frontal tubercle distinct, with median longitudinal groove. Antenna with scape and pedicel yellow; flagellomeres bicolored, brownish black basally, the remainder yellow; all flagellomeres subequal in length; five verticillate setae arising from base of each flagellomere, longest about twice length of flagellomere.

**Thorax:** Pronotum yellow. Scutum yellowish brown with two reddish brown longitudinal stripes bordered by yellow; stripes contiguous anteriorly, narrowly bordered with yellow. Scutum yellowish brown; scutellum brown. Mediotergite quadrate, gray pollinose anteriorly, yellow posteriorly. Pleura evenly yellow, pollinose. Legs with coxae and trochanters yellow, pollinose; remainder of legs brown gradually darker towards apex; apices of femora and tibiae dark. Wings tinged with brown, distinctly patterned with dark brown and white; band before cord conspicuous, white, extending to base of cell  $M_1$ ; dark pigment narrowly present along veins  $CuA_2$ ,  $M_{1+2}$ , m, r-m, basal half of  $CuA_1$ ,  $M_1$ ,  $M_2$ ,  $M_3$ , basal half and distal fourth of  $CuA$ ; pattern in stigmal region of wing restricted, dark brown; dark quadrate area before middle of cell  $CuA$  toward base. Knobs of halteres yellow, stems light brown.

**Abdomen:** Segment 1 brownish yellow; tergites 2 to 5 with basal one-third brownish yellow and remainder brown with paler lateral border; basal rings pale; subbasal impressions inconspicuous; tergite 6 brown; tergites 7 and 8 pale brown. Sternite yellowish brown.



**Hypopygium:** External structures as in Fig. 14, 15. Tergite 8 shorter than tergite 9, broadly emarginate posteriorly; tergite 9 with posterior border produced into two rounded lobes distally separated by a deep U-shaped notch; mesal margins of lobes with abundant short dense spines. Outer dististyle dark brown, nearly parallel-sided in lateral aspect but slightly wider at base, with apex pigmented and bifurcate; outer margin serrate with a dark ridge extending along inner ventral surface toward base. Inner dististyle with beak long and slender; lower beak a dark lobe; outer basal lobe of inner dististyle short, terminating in a dark, rounded lobe.

**Type material.**—Holotype: Male, Papua New Guinea, Northern Province, Myola, Iora Creek, 3 June 1984, Chen W. Young. Paratypes: Two males, topotypic. The holotype and paratype are in the collection of the CMNH. The other paratype is deposited in the Central Reference Insect Collection, Konedobu, Papua New Guinea.

**Etymology.**—This species is named in honor of Mrs. Mary Wible, a long dedicated friend of The Carnegie Museum of Natural History. She has collected specimens for the Section of Invertebrate Zoology over many years, and has provided generous financial support for a wide variety of research projects, including this study.

**Remarks.**—All specimens were collected during the day, resting on the undersides of tree trunks projecting over Iora Creek. The tree trunks were heavily covered with living moss.

#### ACKNOWLEDGMENTS

I would like to thank John Ismay for his help during my collecting trip in Papua New Guinea, Adam Bossert for helping in collecting specimens, Harry Sakulas for making available the facilities at Wau Ecology Institute, and John Rawlins for comments and suggestions on the manuscript. Acknowledgments are due Wayne Mathis (United States National Museum of Natural History), Bruce Townsend (British Museum (Natural History)), Neil Evenhuis (Bernice P. Bishop Museum), Chris Watts (South Australia Museum), and Margaret Debenham (University of Sydney) for their generous loan of type materials. This research was conducted with permission from the Division of Research, Department of Morobe, Papua New Guinea, and was supported by the O'Neil Field Research Fund and the Wible Research Fund, Section of Invertebrate Zoology, The Carnegie Museum of Natural History.

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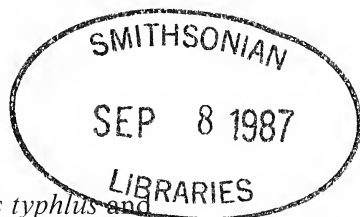
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ARTICLES 8-14

## CONTENTS



- Art. 8. Taxonomic and geographic variation of *Liophis typhlus* and related "green" species of South America (Serpentes: Colubridae) ..... **James R. Dixon** 173
- Art. 9. A new species of *Clinidium* Kirby (Coleoptera: Carabidae or Rhysodidae) from Mexico, and descriptions of the females of two neotropical members of the genus ..... **Ross T. Bell and Joyce R. Bell** 193
- Art. 10. Biosystematic studies in *Stenanthium* (Liliaceae: Veratreae) II. Floral morphology, floral vascular anatomy, geography and taxonomy of the Mexican *S. frigidum* (Schlecht. & Cham.) Kunth ..... **Frederick H. Utech** 197
- Art. 11. Systematics of African bats of the Genus *Eptesicus* (Mammalia: Vespertilionidae). 2. Karyotypes of African species and their generic relationships ..... **Karen McBee, Duane A. Schlitter and R. Laurie Robbins** 213
- Art. 12. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 8. First fossil lizard egg (?Gekkonidae) and list of associated lizards. .... **Karl F. Hirsch, Leonard Krishtalka and Richard K. Stucky** 223
- Art. 13. Taxonomic notes on some African warblers (Aves: Sylviinae) .. **Kenneth C. Parkes** 231
- Art. 14. *Spergenaspis*: a new Carboniferous trilobite genus from North America ..... **David K. Brezinski** 245

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TAXONOMY AND GEOGRAPHIC VARIATION OF  
*LIOPHIS TYPHLUS* AND RELATED "GREEN" SPECIES OF  
SOUTH AMERICA (SERPENTES: COLUBRIDAE)JAMES R. DIXON<sup>1</sup>

## ABSTRACT

The green species of *Liophis* are reviewed. *Liophis typhlus* consists of three subspecies, *L. t. typhlus* (Amazon), *L. t. elaeoides* (Chaco), and *L. t. brachyurus* (Cerrado). *Liophis viridis* consists of two subspecies, *L. v. viridis* (Agreste and Atlantic rainforest), and *L. v. prasinus* (Caatinga). *Liophis jaegeri* is shown to consist of two subspecies, *L. jaegeri jaegeri*, east of the Río Paraná, from São Paulo area of Brazil, to Uruguay and Argentina and *L. j. coralliventris*, from the Río Paraguay basin. *Liophis guentheri* is a valid species from the dry central Chaco of Argentina, Bolivia, and Paraguay. The characters of the recently described species, *L. atriventer* and *L. maryellenae* are summarized. A key is provided for all species of "green" *Liophis*.

## INTRODUCTION

The study of the genus *Liophis*, a long and difficult task, is now nearing completion. The six species presented herein (*L. typhlus*, *L. guentheri*, *L. jaegeri*, *L. viridis*, *L. maryellenae*, *L. atriventer*) form a loosely connected complex of species that have one feature in common, they are all some shade of "green." The green color may be dull to bright, chlorophyll green to leaf green, or with a deep olive cast. Two taxa occasionally have an obscure mid-dorsal stripe of variable width that varies in color from light brown to reddish, and occasionally secondary dark lines as well.

When samples were adequate, each of the six species was examined for geographic variation. No additional specimens of two recently described taxa (*L. atriventer*, *L. maryellenae*) are known, but the species' essential features have been summarized. Of the remaining four species detailed discussions include, where appropriate, the currently recognized name, its synonyms, a discussion of the synonyms, a description of the species, geographic variation, distribution, and comments about pertinent literature.

## SYSTEMATIC ACCOUNT

*Liophis typhlus* (Linnaeus)

*Coluber typhlus* Linnaeus, 1758. Syntypes (not examined)—Royal Museum, Stockholm. Type-locality—Indiis (in error).

*Xenodon isolepis* Cope, 1870. Holotype ANSP (lost). Type-locality—Pebas, Ecuador (=Perú).

*Opheomorphus brachyurus* Cope, 1887. Syntypes ANSP 11202-03. Type-locality—Chupada, Mato Grosso, Brazil.

*Liophis elaeoides* Griffin, 1916. Holotype CM R32. Type-locality—Prov. del Sara, Bolivia.

*Liophis macrops* Werner, 1925. Holotype NMW 23420. Type-locality—Paramaribo, Surinam.

*Nomenclatural comments.*—Several names have been assigned mistakenly to the synonymy of *L. typhlus*. Jan (1863*a*, 1863*b*) and Jan and Sordelli (1866)

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suggested that *L. typhlus* was composed of three varieties in addition to the nominate race, *prasinus*, *gastrostictus*, and *olivaceus*. I have determined that no holotypes exist for any of these varietal names. An examination of Jan's descriptions and Jan and Sordelli's illustrations (1866, Livr. 18, Plate IV, Fig. 3) suggest that the name *prasinus* belongs to *Liophis viridis*. The illustration shows 69 subcaudals, considerably more than the maximum known number of 61 for *L. typhlus*, but well within the known range of 63 to 84 for *L. viridis*. An illustration of a *L. typhlus* by Jan and Sordelli (1866, Livr. 18, Plate IV, Fig. 2) from "Pernambuco," Milan Museum, may represent the variety *gastrostictus*, of Jan (1863a, 1863b). The illustration shows 47 subcaudals, well within the known range of variation in subcaudals for *L. typhlus*. However, the closest localities of *L. typhlus* to Pernambuco are 1300 km to the east and 800 km to the south. The illustration shows dark smudges along the lateral edges of the ventrals, and scattered dark scale edges on the dorsum as well. The illustration and description more closely resemble *L. poecilogyrus* from Pernambuco, and I suggest *gastrostictus* belongs to that species. The Jan name *olivaceus* is without description or illustration. It appears in Jan's (1863a, 1863b) list and key to *Liophis* as a varietal name of *L. typhlus* and should be considered a *nomen nudum*.

Another misapplied name is Wagler's (1824) *Natrix forsteri*. Hoge (1964) first applied it to *L. typhlus* and suggested that the Surinam race be recognized as the nominate taxon and the Brazilian form (by inference) *L. typhlus forsteri*. The type-locality of *L. forsteri* is Salvador, Bahia, Brazil, a locality of considerable distance from any known sample of *L. typhlus*. In addition, the illustration and description of *forsteri* suggests that this name is best applied to *L. poecilogyrus*. The description lists 60 subcaudals for the type of *L. forsteri*. The greatest number of subcaudals recorded in 73 eastern Brazilian individuals of *L. typhlus* is 48. The description of the color pattern of *forsteri* is unlike that of *L. typhlus*, and more similar to that of *L. poecilogyrus*. Hoogmoed and Gruber (1983) examined the holotype of *N. forsteri* in the Munich Museum and gave the subcaudal number as 58/58+1. Although they placed *N. forsteri* as a synonym of *L. typhlus*, I consider *N. forsteri* to be a senior synonym of *L. poecilogyrus*.

Parker (1928) on comparing one of the paratypes of *L. guentheri* (BM 1946.1.5.69) to samples of *L. typhlus* in the British Museum (Natural History), concluded that it "failed to reveal any consequential differences between these two species" and placed *L. guentheri* in the synonymy of *L. typhlus*. Parker erred in his analysis because the ventrals of the specimen he examined (and *L. guentheri* in general) vary from 187 to 197, while ventrals of *L. typhlus* vary from 133 to 172. *Liophis guentheri* is a valid species that is more closely related to *L. viridis* than to *L. typhlus*.

*Distribution.*—*Liophis typhlus* occurs in Amazonian rainforests to an elevation of about 1500 m along the southern and eastern side of the Andes in Colombia, Ecuador and Perú, the rainforests of southern and eastern Venezuela, and similar forests of Guyana, Surinam and French Guiana, and Cerrado and Chaco forests of SE Bolivia, N Paraguay, and SC Brazil (Fig. 1).

*Description.*—The maximum total length is 740 mm in males and 853 mm in females. Body scales are smooth, without apical pits and typically in 19-19-15 rows. Scale rows 3+4 or 4+5 typically fuse on each side of the body between ventrals 68 and 103 ( $\bar{x}$  = 82.2). Scale rows 7+8 or 8+9 usually fuse between ventrals 65 and 104 ( $\bar{x}$  = 83.0). A sample of 48 females and 25 males from Brazil and 49 males and 62 females from other Amazonian localities were analyzed for sexual dimorphism in all quantitative characters and none was found. Ventrals



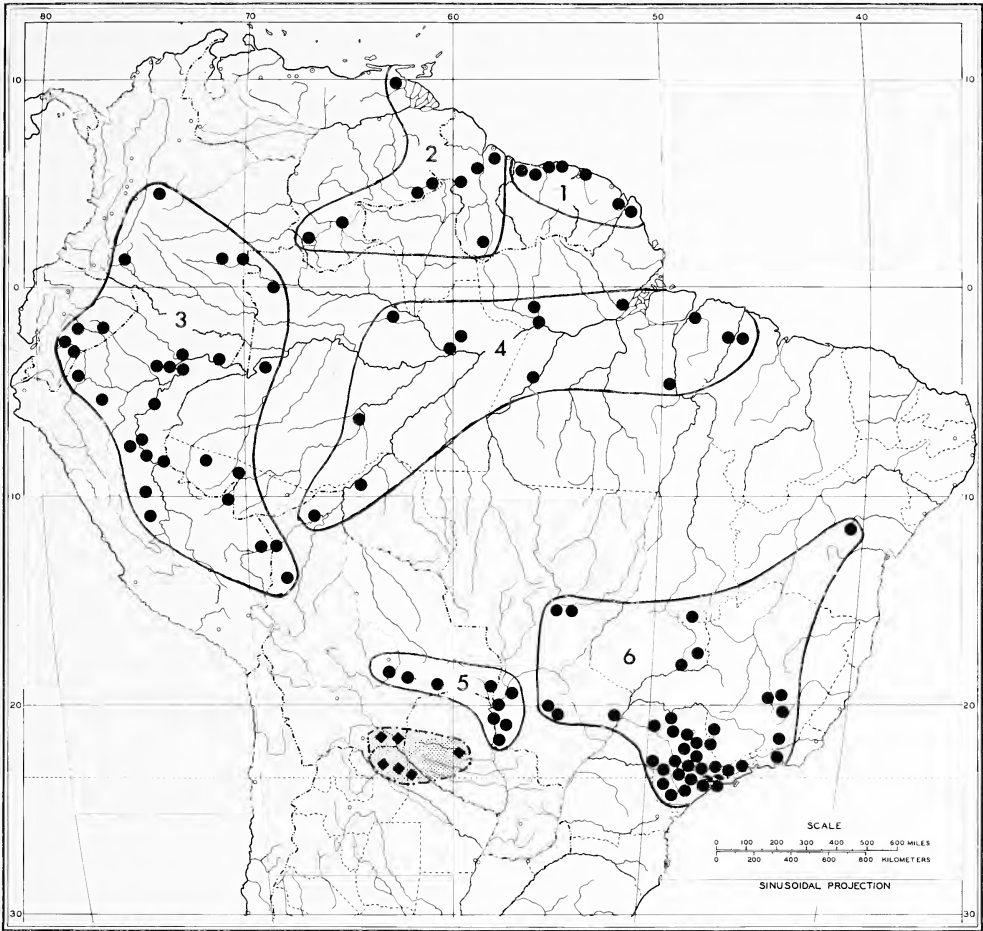


Fig. 1.—Distribution of *Liophis typhlus* (dots) and *L. guentheri* (diamonds, stippled area) in South America. Black lines enclose numbered samples used in the geographic variation analyses.

of 331 specimens numbered 133–172 ( $\bar{x} = 157.1$ ), the number of subcaudals of 307 specimens varied from 41–61 ( $\bar{x} = 49.5$ ). Tail length divided by total length for 105 adult males varied from 0.145–0.206 ( $\bar{x} = 0.169$ ), and for 160 adult females 0.137–0.210 ( $\bar{x} = 0.162$ ). Eye diameter divided by snout length of 127 adults varied from 0.524–0.886 ( $\bar{x} = 0.682$ ). Maxillary teeth for 222 specimens varied from 19–28 ( $\bar{x} = 22.4$ ). The anal plate is divided and the loreal single in all specimens examined.

Head shields vary as follows: supralabials 4–5 (1), 7–7 (3), 7–8 (2), 8–8 (249), 8–9 (5); supralabials entering orbit 4th only (1), 4+5 (252), 3+4/4+5 (2), 4+5/5+6 (4), 4+5/4+5+6 (1); infralabials 5–7 (1), 8–8 (1), 9–9 (10), 9–10 (23), 10–10 (216), 10–11 (5), 11–11 (2), 11–12 (1); preoculars 0–0 (1), 1–1 (256); postoculars 1–1 (3), 1–2 (1), 2–2 (253), 2–3 (3); temporal condition 1+1 (3), 1+2 (242), 1+1/1+2 (12), 1+2/1+3 (3), 0+2/1+2 (1).

The *in situ* length for 69 hemipenes varied from 6 to 13 ( $\bar{x} = 9.0$ ) subcaudals. The organ is slightly bilobed, with each lobe about two subcaudals long. The sulcus spermaticus usually bifurcates about one-third the distance from the base

of the organ. Large spines are present on the asulcate surface of the basal two thirds of the organ, usually becoming much smaller on the lobed part of the organ. A smooth apical disk is present on the outer edge of each lobe and a naked basal pocket is usually present.

*Color in life.*—The dorsal color of some adults is light blue on the head and various shades of green on the body and tail. Amazon samples have reddish brown to black chevron marks over most of the lateral (occasionally middorsal) surfaces of the body. These dark marks are usually prominent in young and juveniles, less so in adults. Some individuals from throughout the range have scattered white scales mixed with the green. Other individuals are uniform green and lack dark chevron marks and blue heads. The venter is usually white or light yellow without darker markings. However, a few individuals have dark smudges or distinct marks ventrolaterally, and the subcaudals may have dark spots or lines.

The juvenile dorsal pattern is variable with some juveniles having distinct black chevrons with a wide black nuchal band. The nuchal band usually fades to an obscure greenish black mark at a total length of 210 mm. Other juveniles from 155–255 mm in total length have a pair of blackish nuchal spots that begin on or at the posterior edge of the parietals, and slant posteroventrally. Occasionally a secondary pair of medium sized dark spots occur on the neck, followed by two rows of paravertebral dark spots and two rows of lateral dark spots to above the vent. Sometimes, the body appears to be reticulated with darker lines on a greenish ground color. One young individual (SVL 225 mm) has distinct spots on scale rows one, two, four, six, and seven, and occasional dark spots along the edges of the ventrals.

*Geographic variation.*—There are three distinct geographic populations of *L. typhlus* that correspond to forest refugia postulated by Vanzolini and Williams (1970), and to some extent, to those of Haffer (1974). The three geographic populations were determined by comparison of the numbers of maxillary teeth, ventrals, subcaudals, the ratio of tail length to total length, and the ratio of the eye diameter to snout length. Six samples were used to determine variation. The samples were chosen by the proximity of individuals to each other and by natural vegetation types, as follows: Sample 1–27 specimens from Surinam and French Guiana; Sample 2–24 specimens from Guyana and Venezuela; Sample 3–53 specimens from Amazonian Colombia, Ecuador, Peru, western Brazil, and Bolivia; Sample 4–29 individuals from Amazonian Brazil; Sample 5–45 specimens from the Chaco of Bolivia and western Mato Grosso, Brazil; and Sample 6–87 specimens from the Cerrado of southeastern Brazil (Fig. 1). The Student's T test was utilized to determine significance of pair-wise comparisons between samples. A Student's T test value of 6.314 or greater is at 95% level of significance or greater. Pair-wise tests for differences between samples 1 and 2, 1 and 4, 2 and 3, 2 and 4 were not significant for any of the characters listed above. Samples 1 and 3 were significantly different from each other in number of ventrals and tail/total length ratio. However, samples 1 and 3 are separated by sample 2, and sample 2 did not differ significantly from either 1 or 3. The significance noted between 1 and 3 is probably an artifact of distance, with sample 2 representing the middle of a cline. Samples 3 and 4 were not significantly different in any characters except ventrals. This may also be an artifact of distance. However, two males from reasonably close localities in Amazonian Bolivia had ventral counts of 140 and 157. Their ventral counts fall near the average of the samples with which they were associated, 143.5 for sample 4, and 154.2, for sample 3 (see Fig. 1). This suggests that a hiatus may exist between samples 3 and 4 in Amazonian Bolivia.

A statistical analysis of ventral number between samples appears to show low to high numbers of ventrals from samples 1 to 4, 1 to 2, 2 to 4, 2 to 3. The samples form an almost closed circle of demes (Fig. 1), with the bottom of the circle open, representing the differences in the Bolivian samples mentioned above. It seems clear that the Amazon samples are closely related, but with a trend to divide the samples into eastern and western demes.

Pair-wise comparisons of samples 4 and 6 suggest a strong differentiation in all characters examined. The differences in the numbers of ventrals, subcaudals, and tail/total length ratios are highly significant between the two samples, with *T* values of 23.8, 19.1, and 15.8 respectively. The number of maxillary teeth differed significantly (*T* value = 7.0) but eye diameter/snout length ratios did not (*T* value = 2.14). The data suggest that the Brazilian Amazon forest and deciduous mesophytic forest samples represent different allopatric taxa. Comparison of samples 3 and 6 shows the same trend, except the number of maxillary teeth is not significant (*T* = 4.91). Pair-wise comparison of samples 4 and 5 shows significant differences in the number of ventrals and maxillary teeth (*T* = 22.03, 10.54, respectively), but not in the number of subcaudals, tail/total length, or eye diameter/snout length ratios (*T* = 2.66, 4.59, 4.62, respectively). Pair-wise comparison of samples 3 and 5 shows significant differences in the number of ventrals, maxillary teeth, and subcaudals (*T* = 9.07, 8.49, 6.36, respectively), but not in the tail/total length and eye diameter/snout length ratios (*T* = 2.96, 6.0). The relative differences between the Amazon samples (1–4) and the two non-Amazon samples (5–6) suggest that the Chaco forest sample from Bolivia is more closely related to the Amazon forest sample than to the deciduous mesophytic forest sample of Brazil. However, both non-Amazon forest samples are very distinct from the Amazon forest samples.

A pair-wise comparison of samples 5 and 6 shows significant differences in the number of subcaudals, maxillary teeth, and tail/total length ratios (*T* = 21.05, 6.43, 12.9, respectively), but not in the number of ventrals or eye diameter/snout length ratio (*T* = 1.36, 3.59). These samples represent different taxa, even though they are relatively close geographically (Fig. 1).

The scale count data and length ratios suggest three distinct populations of *Liophis typhlus*. Samples 1, 2, 3, and 4 represent the Amazon forest form, sample 5 the northern Chaco form, and sample 6 the Cerrado form.

The color patterns of samples 1, 2, 3, and 4 are similar, and the patterns of samples 5 and 6 are identical. The dorsum and head of adult individuals from samples 5 and 6 are chlorophyll green. The young and juveniles have black nape spots and some have four rows of dorsal dark spots. Adults of the Amazon samples have a leaf green to bright green dorsum with diagonal reddish brown to blackish chevron marks along each side of the body. The head may be greenish to bright blue. Young and juveniles are greenish dorsally with bold dark chevron marks and a relatively large black nuchal blotch.

Diagnoses and distributions of the three taxa follow:

***Liophis typhlus typhlus* (Linnaeus)**

*Coluber typhlus* Linnaeus, 1758.

*Xenodon isolepis* Cope, 1870.

*Liophis macrops* Werner, 1925.

**Diagnosis.**—Dorsum usually green with distinct, reddish brown to black chevrons on each side, occasionally fading posteriorly. The dorsal surface of the head

may be greenish to bright blue. The venter is white to light yellow, usually without dark markings. Juveniles have a large black nuchal blotch and dark chevrons. The number of ventrals varies from 133 to 163 ( $\bar{x}$  = 147.3), subcaudals vary from 47 to 61 ( $\bar{x}$  = 54.2), maxillary teeth vary from 20 to 28 ( $\bar{x}$  = 23.6), tail/total length ratios vary from 0.160 to 0.210 ( $\bar{x}$  = 0.184), and eye diameter/snout length ratios vary from 0.510 to 0.861 ( $\bar{x}$  = 0.736).

*Distribution.*—Throughout the Amazon Basin in rainforest, to about 1000 m elevation (see specimens examined).

*Liophis typhlus elaeoides* Griffin

*Liophis elaeoides* Griffin, 1916.

*Diagnosis.*—Dorsally adults are uniform chlorophyll green with a light yellow venter. Juveniles have four rows of dorsal dark spots on a green background, and a pair of black nuchal spots. The number of ventrals varies from 158 to 172 ( $\bar{x}$  = 163.5), subcaudals vary from 49 to 56 ( $\bar{x}$  = 51.9), maxillary teeth vary from 17 to 23 ( $\bar{x}$  = 19.9), tail/total length ratios vary from 0.160 to 0.200 ( $\bar{x}$  = 0.171), and eye diameter/snout length ratios vary from 0.520 to 0.740 ( $\bar{x}$  = 0.620).

*Distribution.*—*Liophis typhlus elaeoides* is known only from the upper Río Paraguay Basin, which includes the mesic Chaco forests of southeastern Bolivia, northern Paraguay, and western Mato Grosso, Brazil (see specimens examined).

*Liophis typhlus brachyurus* (Cope)

*Opheomorphus brachyurus* Cope, 1887.

*Diagnosis.*—Adults are uniform green dorsally with a light yellow venter. Juveniles have four rows of dark dorsal spots on a green background and a pair of black nuchal spots. The number of ventrals vary from 151 to 171 ( $\bar{x}$  = 162.2), subcaudals vary from 40 to 49 ( $\bar{x}$  = 44.4), maxillary teeth vary from 18 to 24 ( $\bar{x}$  = 21.5), tail/total length ratios vary from 0.140 to 0.160 ( $\bar{x}$  = 0.149), and eye diameter/snout length ratios vary from 0.55 to 0.81 ( $\bar{x}$  = 0.675).

*Distribution.*—*Liophis t. brachyurus* occurs in deciduous mesophytic forests of southeastern Brazil, and in the Campos Cerrado forests of east-central Brazil (see specimens examined).

*Comments.*—Two recent papers by Miranda and Couturier (1983, 1984) comment on the presence and geographic variation of *L. typhlus* in Argentina. I have neither examined their specimens, nor located specimens of *L. typhlus* from Argentina in other museums. I believe they may have erred in identification of their specimens. Photographs presented by Miranda and Couturier (1984) suggest that they may have confused *L. miliaris* and *L. poecilogyrus* with *L. typhlus*.

Short works on the distribution and taxonomy of *L. typhlus* are Hoge (1964), Amaral (1931, 1935, 1949), Gans (1960), Parker (1928, 1935), Peters (1960), Peters and Orejas-Miranda (1970), Roze (1966), and Prado and Hoge (1948). Peters (1963) compared the maxillary teeth of *L. typhlus* with those of other species of *Liophis*.

*Specimens examined.*—(*Liophis typhlus typhlus*) BOLIVIA, Beni: Ixiamus AMNH 22457; Rio Beni AMNH 22270. BRAZIL, Acre: Alto Purus MZUSP 2498; Porto Walter MZUSP 7390. Amapa: Cuidade Oiapoque IB 13780, 13783; Serro do Navio KU 97873–97875. Amazonas: Barreira do Matupiri, on the Río Madeira MZUSP 5912; Carvoeiro AMNH 36167; Costa Altamira on the Río Japura MZUSP 6600; Lago Alexo MCZ 3290; Manaus MZUSP 3051, 3797; Reserva INPA MZUSP 7606, 7619; Santa Isabel on the Río Negro USNM 83532; São Paulo de Olivença AMNH 53311;

Tapaua MZUSP 5770; no specific locality UZM 601223. *Maranhao*: Aldeia Aracu Igarape Gurupi-Una MZUSP 4303, 4826. *Para*: As Pedras, on the Río Cuminá-Miri MZUSP 5103; Belém IB 15667; Canindé, on the Río Gurupi MZUSP 4267, 4285; near Maraba, Serrando Norte KU 124608; Oxiximina MZUSP 4796; Uruã, Parque Nac. da Amazonia, on the Río Tapajos MZUSP 7838. *Rondonia*: Porto Velho MZUSP 3690. COLOMBIA, *Macanal*: Río Garagoa MCZ 27339. *Meta*: Villavicencio IB 8589. *Vaupés*: Timbo UTA R3805; Yapima UTA R5033. ECUADOR, *Napo-Pastaza*: Alpayaca FMNH 4069, UMMZ 89020-22; Andoas AMNH 41949; Baños+Canelos AMNH 35892; Chamala-Nor-mandia-Río Bamba AMNH 35929-35930; Jarayacu AMNH 28796; Macas and Vicinity AMNH 35838-35839; 82 km ESE Macas AMNH 114616; Río Bamba AMNH 15209, 15213, 23296, 23302, 28848; Río Pastaza MCZ 36966; Santa Rosa, El Tigre AMNH 49165. FRENCH GUIANA (CAY-ENNE), Mana USNM, 6172; Saul MCZ 149399; near Sophie MCZ 77510-77511. GUYANA, Bartica-Potaro road BM 1954.1.3.64; 82 km S Bartica BM 1934.11.1.125; Berbice BM RR1964; Demerara River, Lama Creek AMNH 36106; Essequibo, near Lethem USNM 146376; Kartabo AMNH 21335, 98197-98198; Matali AMNH 61542; Rupununi District, north of Acaraí Mountains, west of New River KU 69826-69828; Rupununi District, north of Acaraí Mountains, west of New River KU 69826-69828; no specific locality MNHG 279.38. PERÚ, *Amazonas*: Caterpiza, Río Caterpiza USNM (RWM field series) 14995, 15033, 14185-15186. *Junin*: Río Perene MCZ 42434. *Loreto*: Balta LSUMZ 14584; Centro Union TCWC 44682; Cerros de Contaya, on the Río Tapiche AMNH 53376; Contamana on the Río Ucayali AMNH 52130; Estirón on the Río Ampiyacu MZUSP 4394; Iquitos AMNH 52734; 53118, 53284, 53667, 53696, 53735, 53771, 53773, 53876, 53923, 53949, 54321, 54354, 54483, 54894, 56109; Moropon TCWC 38049, 44294; Orellana (Reforma) AMNH 54957, USNM 127124; Pampa Hermosa on the Río Cushabatay AMNH 55409, 55415, 55442, 55791, 55885, 56003; Panya AMNH 53249; Requena (Monte Carmelo) AMNH 55600, 55626; Royaboya AMNH 52483, 53110, 53288, 55695; San Antonio on the Río Itaya AMNH 52920, 53667, 53693, 53696, 53735; Shiriara, on the Río Nanay AMNH 56075; Trapiche-Utuquinia AMNH 52195; Yanamono TCWC 40542-40543. *Madre de Dios*: Río Heath, 50 km S Puerto Pardo LSUMZ 36778-79; mouth of Río Torre on the Río Tambopata LSUMZ 394244. *Pasco*: Iscozazin Valley LACM 76805. *San Martin*: Moyobamba BM 74.8.4.59, 94.8.4.64. SURINAME: Charlesburg AMNH 104624; Coppename River MCZ 152203, 152205, 152633-152634; Jaraweg TCWC 60543, 60756; Paramaribo AMNH 8146, 8682, MCZ 16401; Potribo CM 44302; Sipaliwini Airstrip CM 84667, MCZ 152636; Zanderi (Airport) MCZ 152635. VENEZUELA, *Amazonas*: Arabopó UMMZ 85279; Arocoima Caños MCZ 38541; Mount Duida region AMNH 36617, 36620. *Bolivar*: El Manteco TCWC 60168; no specific locality MHNLS 1632.

(*Liophis typhlus elaeoides*) BOLIVIA: *Cochambamba*: Villa Tunari UMMZ 153095. *Santa Cruz*: Buenavista CM R2696, R2698, R2701, R2704, R2869, R2886, R2930, R2931; UMMZ 67967-67968, 67969(2), 67970(3); Buenavista, near Río Colorado CM R2860, R2865, R2955; Santa Cruz LSUMZ 11825; Santa Cruz de la Sierra CM R32 (holotype), R44, R59, R91, R94, R95, R97, R98, R99, R102, MCZ 11860, MZUSP 6474; San Jose de Chiquitos CM 34842. No specific locality: CM R2938-R2939, FMNH 195898, HCD 2820, 2822, TCWC 55290. BRAZIL: *Mato Grosso*: Corumbá, near Urucum Mountains CM 34841; Fazenda Bela Vista of the Ilha Insua MZUSP 7264; Fazenda Vacurizai of the Río Paraguai MZUSP 7266; Generalso Ponce, Corumba IB 25954; Maleta IB 14975; Porto Murtinho IB 26177-78.

(*Liophis typhlus brachyurus*) BRAZIL: *Bahia*: Mira Serra, 41 km from Morro de Chapéo MZUSP 7554. *Goaiz*: Araguari IB 6851; Fazenda Lucushac, on the Río Verde IB 13060. *Mato Grosso*: Arapua IB 9939; Aquidauana MZUSP 33589; Chapada ANSP 11202-11203, BM 92.420.13; Taugará da Serra IB 24543; Taunay IB 7674; Urucum, near Corumbá BM 1928.1.12.3. *Minas Gerais*: Horto Forestal IB 10493; Irma Badur IB 6933; Itambe do Mato Dentro MZUSP 8061; Juiz de Fora IB 25190, 26685; Machado IB 16303; Santa Rita do Extrema IB 5540, 5562. *Rio de Janeiro*: Nova Friburgo IB 10516. *São Paulo*: Araraquara IB 231; Atibaia IB 21376, 27081, 27201; Barra Assugnui IB 29042; Barretos IB 5030; Baureri IB 7212; Bauru MZUSP 823; Boraceia MZUSP 4227; Botucatu MZUSP 2410, 2412; Buri IB 6718, 6763, 12313; Campo Limpo IB 805, 6452, 10265-10267, 24903-24904; Capão Bonito IB 23465; Cascavel MZUSP 824; Conde do Pinhal IB 9975; Cotia IB 5743, 6935, 7140, 9906, 19906, 23236, 23377, 24542, 32627; Curupá IB 7061; Dona Catarina IB 22598; Elias Fausto IB 232, 319, 392, 578, 791, 10461; Elihu Root IB 234; Engenheiro Cesar de Souza IB 8338; Ferraz de Vasconcelos MZUSP 2487; Guarulhos IB 23726-23727; Horto Florestal IB 10493; Ibiuna IB 12252, 23794; Ipanema IB 230, 235; Itaguá IB 4813; Itapecerica da Serra IB 7794, 19682, 25040, 25043; Itapetininga IB 24565; Itapolis IB 7956; Itaquera IB 30758; Itaquaquecetuba IB 18349; Itirapina IB 6655; Jaraguá IB 21381; Jarinú IB 10292; Lauro Muller IB 10533, 10556, 10559; Leme IB 236, 547; Mairinque IB 7373, 7461; Mairipora IB 28603; Mogi das Cruzes IB 12592, 19658, 23547, 24881, 28284, MCZ 39415, MZUSP 6460; Osasco IB 12500, 27910-27911; Pederneiras IB 6938; Pindamonhangaba IB 1257; Piraju MCZ 39416; Promissão IB 9969; Ribeiras Pires IB 19596; Río Claro IB 7277, 10296;

Santa Adélia IB 6909; Santa Ernestina IB 27969, MZUSP 2479; São Carlos IB 10016; São Jose do Rio Pardo IB 5444; São Jose dos Campos IB 21348; São Paulo IB 797, 7142, 12980, 12993, 16223, 16900, 18854, 25295, 27497, 28458, MCZ 17956, MZUSP 817–820, 2388, 3338–3339, 3695, USNM 69238–69239; Suzano IB 19104; Valinho IB 6719; Vinhedo IB 2915; no specific locality IB 233, 237, 797, 840, 4745, 5491, 5642, 6950, 9775, 10581, 12112, 17777.

### *Liophis guentheri* Peracca

*Liophis guentheri* Peracca, 1897. Six syntypes (Five lost ?), Mus. Comp. Anat., Torino. Type locality—Caiza, Bolivia.

*Comments.*—*Liophis guentheri* has resided as a synonym of *L. typhlus*. Parker (1928) compared one of the syntypes (now BM 1946.1.5.69) with a specimen of *L. typhlus*, and suggested it “failed to reveal any consequential differences between the two species.” However, no overlap in the number of ventrals occurs between the two species. An unnumbered British Museum specimen from an unspecified locality in Bolivia is similar to the numbered syntype in the collection of the British Museum in its state of preservation, and may well be one of the five missing syntypes that were housed in the Museum of Zoology and Comparative Anatomy in Torino.

*Distribution.*—*Liophis guentheri* apparently is restricted to the central Chaco of Bolivia, Argentina and Paraguay (Fig. 1).

*Description.*—The following description is based on six adult females and three adult males. The maximum total length of males examined is 655 mm, of females 723 mm. Peracca (1897) gave 890 mm as the maximum total length but did not indicate the sex. Scale rows are 19-19-15, smooth, without apical pits; a reduction of the third and fourth scale row occurs between ventrals 98–118 ( $\bar{x}$  = 106.9), and reduction of the seventh and eight scale rows between ventrals 99–112 ( $\bar{x}$  = 106.1). The number of ventrals varies from 187 to 197 ( $\bar{x}$  = 191.6), the number of subcaudals from 53 to 57 ( $\bar{x}$  = 54.6) (only five with complete tails). The number of maxillary teeth varies from 20 to 22 ( $\bar{x}$  = 20.9). Head scales are as follows: supralabials 7-8 (1), 8-8 (7), 8-9 (1); supralabials entering orbit 4+5 (8), 4+5/5+6 (1); infralabials 9-9 (1), 9-10 (1), 10-10 (5), 10-11 (2); preoculars 1-1, postoculars 2-2, loreals 1-1, temporals 1+1 (1), 1+2/1+1 (1), 1+2 (7). The anal plate is divided. The tail/total length ratio varies from 0.152–0.168 ( $\bar{x}$  = 0.159); eye diameter/snout length ratios vary from 0.467 to 0.578 ( $\bar{x}$  = 0.502).

The hemipenis is nine subcaudals long, with the sulcus spermaticus dividing at the level of the third subcaudal, slightly bilobed (about one and a half subcaudals), and very spinose. The smooth apical disks are pronounced.

The general dorsal color is light blue in preservative, but Peracca (1897) states that living specimens are immaculate green dorsally and yellowish white ventrally. The ventrals and subcaudals are usually immaculate white in preservative. In two preserved specimens there are dark flecks and/or spots on the outer edges of the ventrals. Flecks cover all ventrals in one specimen and three fourths of the ventrals in the other.

*Specimens examined.*—ARGENTINA: *Salta*: Hickmann IML 105, 303; Luna Muerta IML 301; *Formosa*: Ingeniero Juarez IML 422, 490. BOLIVIA: no specific locality IB 1177, BM (unnumbered); *Chaco*: Caiza BM 1946.1.5.69. PARAGUAY: *Chaco*: Loma Plata KU 73454.

### *Liophis viridis* Günther

*Liophis viridis* Günther, 1862. Holotype, BM 1946.1.5.69. Type-locality—Brazil, Pernambuco, no specific locality.

*Liophis typhlus prasina* Jan and Sordelli, 1866. Holotype (lost?). Type-locality—Brazil.

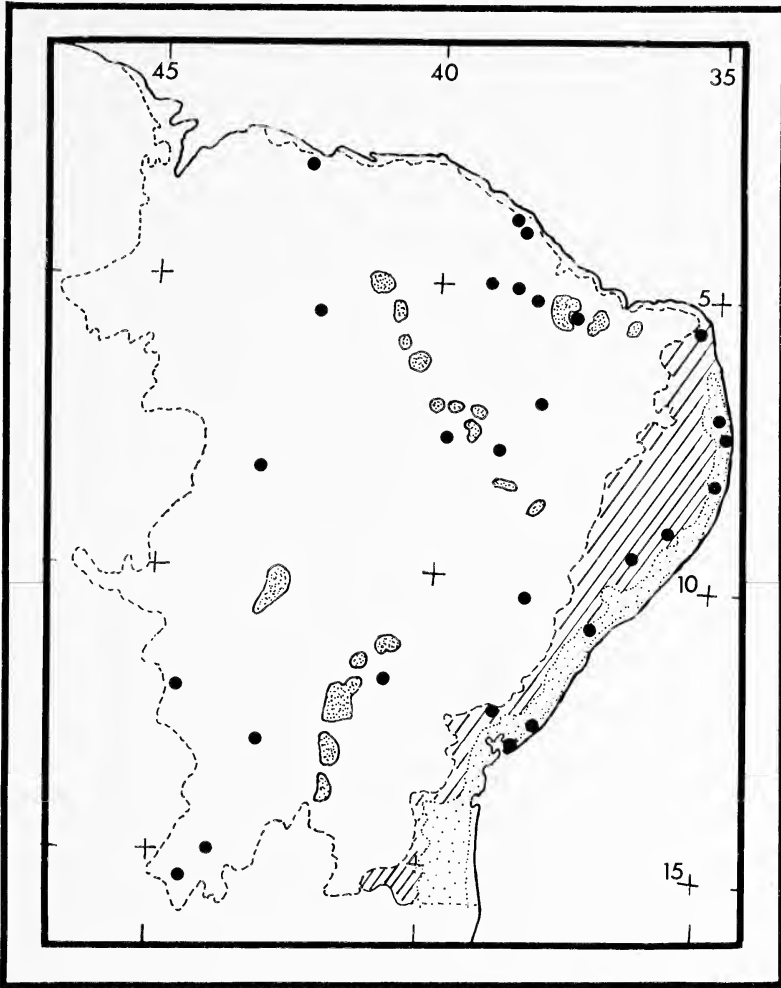


Fig. 2.—Distribution of *Liophis viridis* in northeastern Brazil. Dots within the diagonal lines (Agreste plant formation) and lightly stippled area (Atlantic rainforest formation) represent the Agreste-Atlantic Rainforest sample. Dots within the dashed line (Caatinga plant formation) represent the Caatinga sample. Densely stippled areas within the Caatinga formation represent enclaves of the Cerrado plant formation.

*Distribution.*—Known only from the Caatinga, Agreste, and Atlantic rainforest vegetation communities of northeastern Brazil (Fig. 2).

*Description.*—The following description of *L. viridis* is based on 159 individuals from throughout the range. The maximum total length of males is 595 mm, and of females 670 mm. The scale rows are 19-19-17, smooth, and with one apical pit. The reduction to 17 rows occurs through a fusion of scale rows three and four between ventrals 98 and 121 ( $\bar{x} = 110.0$ ). Sexual variation was not detectable even in large samples, therefore all scale data were combined for intrasample comparisons. Ventrals vary from 169 to 202 ( $\bar{x} = 186.0$ ); subcaudals from 63 to 84 ( $\bar{x} = 74.1$ ). Tail/total length ratios of adults vary from 0.193 to 0.249 ( $\bar{x} = 0.221$ ). The eye/snout ratios of adults vary from 0.500 to 0.684 ( $\bar{x} = 0.562$ ).



Maxillary teeth vary from 17 to 24 ( $\bar{x}$  = 20.2), with the last two teeth enlarged and separated from the remainder by a decided gap. The anal plate is divided in all specimens examined.

Head scales vary as follows: supralabials 8-8 (156), 8-9 (2), 9-9 (1); supralabials entering orbit 4+5 (155), 4+5/5+6 (3), 4+5+6/5+6 (1); infralabials 8-9 (2), 8-10 (1), 9-9 (2), 9-10 (4), 10-10 (144), 10-11 (4), 11-11 (2); preoculars 1-1 (156), 1-2 (2), 2-2 (1); postoculars 1-1 (1), 2-2 (157), 2-3 (1); loreals 1-1 (159); temporals 1+1 (12), 1+1/1+2 (21), 1+2 (145), 1+2/1+3 (1).

The hemipenis is 9 to 13 ( $\bar{x}$  = 10.8) subcaudals long (*in situ*) and bilobed for 1.5 to 3 subcaudals. Large spines occur from the base to the proximal part of the lobe. Spines about one half the size of the basal spines occur from the lobe to the distal end. The sulcus spermaticus is divided near the base of the lobes. The smooth apical disk is relatively large.

The dorsum is bright green in life. Young and small juveniles may have black bands in the nape region followed by a series of black spots arranged in four linear rows, primarily along scale rows three and four, and seven and eight. The number of spots is variable in any row, varying from 36 to 60, especially in individuals from 180 to 220 mm in total length. Some young have only a nape band, immediately followed by one pair of dorsal spots. Occasionally young have a black lateral tail stripe. Spots on juveniles from 240 to 370 mm in total length are faded posteriorly. Normally all individuals over 400 mm in total length are uniform green and the belly and subcaudals are immaculate white. Vanzolini et al. (1980) give a very good color description of living individuals of this species.

*Geographic variation.*—A Caatinga sample and an Agreste-Atlantic rainforest sample were formed from three coastal subsamples and two inland subsamples of *L. viridis* (Fig. 2).

The Caatinga sample is significantly distinct ( $T$  = 13.4) from the Agreste-Atlantic rainforest sample in having a higher number of ventrals, 181–202 ( $\bar{x}$  = 189.8), versus 169–188 ( $\bar{x}$  = 179.6), and a higher number of ventrals ( $T$  = 6.44) at the 19–17 reduction site 102–124 ( $\bar{x}$  = 114.6) versus 98–116 ( $\bar{x}$  = 106.6). Other scale and tooth characters are not significantly different between samples.

One specimen from Jeremoabo, Bahia, and five specimens from Mina de São Felix do Amianto, Bahia, are known from the eastern part of the Caatinga. Their taxonomic features more closely approximate those of the Agreste-Atlantic rainforest sample than others from the Caatinga. Although the samples are small I suspect that they may represent intergrades between two well-defined subspecies.

The Caatinga sample (Fig. 2) does not have a formal name. However, Jan (1863*a*, 1983*b*) and Jan and Sordelli (1866) mention a varietal name associated with *L. typhlus* that belongs to *L. viridis*. It was originally cited as a varietal name (without description) by Jan (1863*a*, 1863*b*) but was illustrated by Jan and Sordelli (1866) and their iconotype represents the only description. Jan (1863*a*, 1863*b*) recorded two specimens of the variety, one from “Fernambuco” in the Milan Museum, and one from “Brasile” in the Stuttgart Museum. Jan and Sordelli illustrated the latter specimen, thus it becomes the holotype (by inference). However, neither specimen now can be located. I cannot definitely assign the name to either of the two populations that require recognition. However, the genus is already overburdened with excessive synonyms and I propose that Jan and Sordelli’s varietal name, *prasinus*, as proposed in the combination *L. typhlus prasinus*, be recognized as the proper name for the Caatinga population of *L. viridis*.



*Liophis viridis viridis* Günther

*Liophis viridis* Günther, 1862.

**Diagnosis.**—Dorsally adults are leaf green to bright green, and pale cream to white ventrally. Juveniles have a black nape band followed by a various number of paired black dorsolateral spots. The number of ventrals varies from 169 to 188 ( $\bar{x}$  = 179.6), and reduction occurs between ventrals 98 and 116 ( $\bar{x}$  = 106.6).

**Distribution.**—*Liophis v. viridis* occurs in the Atlantic rainforest and the Agreste forest from Recife, Pernambuco, east and south to Salvador, Bahia, Brazil.

*Liophis viridis prasinus* Jan and Sordelli

*Liophis typhlus prasina* Jan and Sordelli, 1866.

**Diagnosis.**—Adults are bright green, with an immaculate cream to white venter. Juveniles have bright green dorsums with a single black nape band, or with four parallel rows of 35 to 60 black spots per row. Occasional juveniles have a pair of posterior, lateral black stripes that extend onto the tail. The number of ventrals varies from 181 to 202 ( $\bar{x}$  = 189.8), with the reduction occurring between ventrals 102 and 124 ( $\bar{x}$  = 114.6).

**Distribution.**—*Liophis v. prasinus* occurs from João Pereira, Maranhão in northeastern Brazil, south to São Francisco, Minas Gerais, then northeast to about Parauagua, Rio Grande do Norte, Brazil.

**Comment.**—Vitt (1983) found *Hyla rubra*, *Physalaemus cuvieri*, and several unidentified leptodactylids in 14 stomachs of *L. viridis*. Vitt examined 16 gravid females and determined that *L. viridis* produces continuous clutches throughout the year. Ovarian clutch size varied from two to six ( $\bar{x}$  = 3.69) eggs.

Short taxonomic works for *L. viridis* include Cordeiro and Hoge (1973), Gomes (1918), and Schmidt and Inger (1951). Vanzolini et al. (1980) give an excellent summary of scale data, color of young and adults, and brief biological notes on a Caatinga sample.

**Specimens examined.**—"SOUTH AMERICA": CM R281. BRAZIL: no specific locality FMNH 5694, MZUSP 815, NHMW 20739; no specific state, Parauagua ZMUC 601250. *Algoas*: Quebrangulo MZUSP 3453. *Bahia*: No specific locality FMNH 5721, IB 3200, MCZ 2946, 147217–147218. Assu da Torre IB 980, Brreiras UMMZ 108712–108716, Bom Jesus de Lapa CM R344, UMMZ 108711, Feiro de Santana KU 29478, Itapoan MZUSP 5713, Jeremoabo MZUSP 5738, Mina de São Feliz do Amianto IB 28170–28172, 28215–28216, Salvador BM 90.1.27.2, 1924.9.20.26, MZUSP 2838–2839. *Ceara*: Acude Amanari Maranguape MZUSP 3450, Boa Viagem IB 20200, Caxueira ZMUC 3342(3), Coluna MZUSP 5319–20, Limoeiro do Norte IB 12776–12777, Uruqué IB 20142. *Maranhão*: Lagoa de João Pereira CM R316. *Minas Gerais*: Januaria UMMZ 108705–108709, São Francisco UMMZ 108710. *Parahyba*: Coremas MZUSP 3451, João Pessoa MZUSP 7976–7977, 7999, 8262, UFFB 139, 141, 143, Mamanguape MZUSP 3456. *Pernambuco*: no specific locality MANH 4448, BM 1946.1.2.69, 80.11.25.4, 80.11.25.8, MCZ 1447, 146945–146947, Agrestina MZUSP 4925, 4942, 4946, 4965, 4970, Exu MZUSP 6693–6699, 6700–6718, 7071–7091, 5 km E Exu MZUSP 6950, 13 km Exu MZUSP 6940–6943, 5 km N Exu MZUSP 6920–6921, 11 km S Exu MZUSP 7092, Ponta de Pedras MZUSP 5177, Recife DEH 624, 517, 526, LSUMZ 36787. *Piauí*: Acude Peri-Peri MZUSP 3424, 3427–3429, 3433, 3435–3438, 3441, 3443, 3445, Terezina IB 360, 473, 1210–1214, Valença MZUSP 5814. *Rio Grande do Norte*: Ceará Mirim CAS 49320. *São Paulo*: Leme IB 543 (in error). *Sergipe*: Aracaju IB 22458, Maruim ZMUC 601251, Santo Amaro das Brotas MZUSP 6985, 7306.

*Liophis jaegeri* (Günther)

*Coronella jaegeri* Günter, 1858. Syntypes—BM 1946.1.9.12, 1946.1.5.78. Type-locality—Brazil, no specific locality.

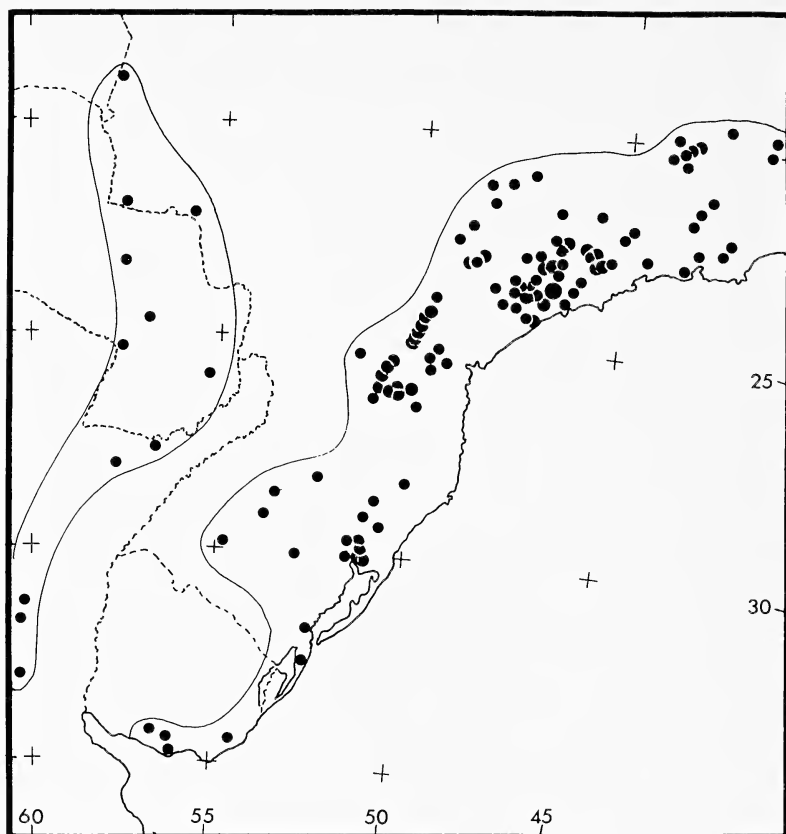


Fig. 3.—Distribution of *Liophis jaegeri* in southeastern South America. Black lines enclose samples utilized in the analyses of geographic variation. The large black dot represents several overlapping localities.

*Liophis dorsalis* Peters, 1863. Type-locality—Brazil, no specific locality.

*Aporophis coralliventris* Boulenger, 1894. Type-locality—Island north of Concepcion, near San Salvador, north Paraguay.

*Rhadinaea lineata* Jensen, 1900. Type-locality: Taboleiro Grande, Minas Geiras, Brazil.

*Misapplied synonym.*—*Rhadinaea dichroa* Werner (1899) has been in the synonymy of *L. jaegeri* since 1972 (Peters and Orejas-Miranda, 1972). However, an examination of the type description reveals that the holotype has 19 midbody scale rows, 159 ventrals, and 50 subcaudals. The dorsum is brown with the bases of the scales white and the posterior edges black. It also has a tail/total length ratio of 0.185. The description is identical to that for *Liophis poecilogyrus caesius*, a form common to the Chaco of Bolivia, Argentina, Paraguay and Brazil, and I assign it to that species.

*Distribution.*—*Liophis jaegeri* occurs from about 19°S latitude in Brazil, to about 35°S latitude in Uruguay and Argentina, west to about 61°W longitude, along the Río Paraguay basin in Argentina, Paraguay and Brazil (Fig. 3).

*Description.*—Some 415 individuals of *L. jaegeri* were examined and full data taken on 160. Tail/total length ratios were recorded for over 400 individuals. The maximum total length of males is 539 mm, of females 676 mm. Dorsal scales

are smooth, in 17 rows, normally without reductions, and without apical pits. When reductions are present (15 individuals), they occur with a fusion of scale rows three and four on one or both sides of the body, reducing to 15 or 16 between ventrals 88 and 141 ( $\bar{x} = 121.2$ ).

Sexual variation in the number of ventrals, subcaudals, maxillary teeth, and tail/total length ratios is absent, therefore the samples were combined for statistical analysis. The number of ventrals of 160 individuals varies from 146 to 169 ( $\bar{x} = 157.5$ ), and subcaudals from 52 to 75 ( $\bar{x} = 61.7$ ). The number of maxillary teeth varies from 22 to 29 ( $\bar{x} = 25.6$ ). The tail/total length ratios varies from 0.181 to 0.268 ( $\bar{x} = 0.221$ ). The number of palatine and pterygoid teeth were recorded for one individual and they were 10 and 25 respectively.

Head scales are as follows: supralabials 6-7 (1), 7-7 (1), 7-8 (4), 8-8 (147), 8-9(4), 9-9 (1); supralabials entering the orbit 3+4 (1), 3+4/4+5 (3), 3+4+5/4+5 (1), 3+4+5/4+5+6 (1), 4+5 (148), 4+5/4+5+6 (2), 4+5+6 (1); infralabials 8-8 (3), 8-9 (4), 8-10 (2), 9-9 (5), 9-10 (24), 9-11 (1), 10-10 (112), 10-11 (5); preoculars 1-1 (155), 1-2 (2), 2-2 (1); postoculars (2-2) and loreals (1-1), temporals 1+1 (5), 1-1/1-2 (11), 1+2/2+1 (1), 1+2 (141); eye diameter/snout length ratios of 20 adults varies from 0.533 to 0.844 ( $\bar{x} = 0.655$ ). The anal plate is divided in all specimens. Hemipenial length varies from 7 to 13 ( $\bar{x} = 10.3$ ) subcaudals.

A hemipenis extending 12 subcaudals has the sulcus spermaticus divided at the level of the 6th subcaudal, and the lobes begin at the level of the 9th subcaudal. Large spines occur on the asulcate side of the hemipenis to the edge of the large, smooth, apical disk. Calyces appear to be absent and only a weak basal naked pocket is present.

The general dorsal color is dull green, olive green, or olive brown. The venter normally is rose or coral red, with or without lateral dark marks on the edges of the ventrals. In life there is a reddish brown to olive brown stripe covering scales rows 8 through 12, and frequently parts of scale rows 7 and 13. The stripe varies in width from 5 to 10 rows of scales. Occasionally dark brown spots occur on the posterior edge of rows 3, 4, 5, and sometimes along scales rows 7 and 8. The upper and lower lips, throat and anterior ventrals may be cream or yellowish. Color descriptions also are presented by Miranda et al. (1982).

*Geographic variation.*—160 individuals were grouped into nine geographic samples. Three samples were located in the Río Paraguay basin in a north/south line, and six samples were scattered from Uruguay to southeastern Brazil, more or less in a north/south line. Using univariate statistics, the number of ventrals, maxillary teeth, subcaudals, and tail/total length ratios were analyzed for intra and inter-sample variation. The two numbers that follow a mean value are the standard deviation and standard error, respectively. In addition, Student's T Test values were used to determine significance at the 95% level, in a pair-wise sample comparison. No significant differences in pair-wise comparisons exist for any of the samples arranged in the two north to south lines. There are trends in both lines to increased number of ventrals and subcaudals from north to south. The trend for maxillary teeth is reversed, with numbers decreasing from north to south. Pair-wise comparisons of the Student's T Test values for the number of ventrals, maxillary teeth and tail/total length ratios of eastern and western samples were not significant. However, a significant difference between eastern and western samples in the number of subcaudals exist. Subcaudals of the combined three western samples ( $N = 18$ ) vary from 63 to 75 ( $\bar{x} = 68.5$ , 3.8, 0.9), while the combined six eastern samples ( $N = 110$ ) vary from 52 to 71 ( $\bar{x} = 60.4$ , 3.4, 0.3).

the tail/total length ratios of the western samples vary from 0.214 to 0.268 ( $\bar{x}$  = 0.231, 0.29, 0.07) and those of the eastern samples from 0.193 to 0.248 ( $\bar{x}$  = 0.221, 0.13, 0.01). This suggests that the subcaudals are smaller in the western sample, hence more subcaudals are present on a tail about the same length as in the eastern sample. The eastern and western samples are separated by the Río Uruguay and Río Paraná basins and appear to be allopatric (Fig. 3). However, additional collecting may reveal parapatry of the samples.

Since the number of subcaudals is significantly different between the two samples, I propose recognition of the following taxa:

*Liophis jaegeri coralliventris* Boulenger

*Diagnosis.*—Dorsum ground color leaf green, sometimes with a middorsal brownish red stripe five to six scale rows wide, extending from the nape to the tail, and with a dark brown line on scale row three on each side of the body. Venter rose to red, with or without ventrolateral blackish marks on the edges of the ventrals. Subcaudals vary from 63 to 75 ( $\bar{x}$  = 68.5).

*Distribution.*—Known only from the Río Paraguay Basin of Argentina, Paraguay, and Brazil (Fig. 3).

*Liophis jaegeri jaegeri* (Günther)

*Liophis dorsalis* Peters, 1863.

*Rhadinaea lineata* Jensen, 1900.

*Diagnosis.*—Dorsum olive green, grayish green or leaf green, often with a mid-dorsal brownish or reddish stripe six to eight scale rows wide, sometimes with dark dots along scale row four, and occasionally along scale rows three and five. Venter rose or reddish, with or without ventrolateral black marks on the edges of the ventrals. Subcaudals vary from 52 to 71 ( $\bar{x}$  = 60.4).

*Distribution.*—Known only from the east side of the Río Parana Basin east to the Atlantic coast, and from Uruguay north to 19°S latitude in Brazil (Fig. 3).

*Comment.*—Little is known about the natural history of this species. I have found 7 and 9 eggs in two specimens, and Miranda et al. (1982) indicated that the average number of eggs for this species is about 14. Miranda et al. also indicated that the species is diurnal, frequently found in humid places, and eats small frogs. Notations on some field tags suggest that the species also occurs in brushy areas, has been found “crossing dirt roads” and “in a puddle of a cow track in low campo, 10:30 am, 84°F, and in full sun.”

Dixon (1985) presented evidence that *L. jaegeri* and *L. maryellenae* hybridize in an area near Belo Horizonte, Minas Gerais, Brazil. Additional material from the latter area has not been located, and the hybrid zone remains undefined.

*Specimens examined.*—(*L. jaegeri coralliventris*). ARGENTINA, Corrientes: Gral Paz, esteros de la Santa Lucia IML 802, Ituzaingo IML 1180. Rosario: Rosario MNHP 1899.6–7. Santa Fe: Bañados del Rincon CM 39130, Buenos Aires MNHP 676–50, Laguan Guadalupe CM 39128. BRAZIL, Mato Grosso: Corumba IB 26575, Río Apa UMMZ 108761, upper Río Parana/Río Paraguay UNM 68831. PARAGUAY, Asuncion BM 1930.11.27.208, Buenavista, NE of Caaguarzu MCZ 34204, Isla Concepcion BM 1946.1.5.85, Primavera BM 1960.1.2.84–85, 1960.1.3.40, 1962.81.

(*Liophis jaegeri jaegeri*). BRAZIL, Minas Gerais: no specific locality MCZ 20715–20716. Belo Horizonte UMMZ 109069, Campo Alegre IB 196, Coronel Fabriciano IB 22993, Imbuzeiro USNM 100676, Itapeva IB 41126–41127, Juiz de Fora IB 30728, 33501, Mutum IB 3802, Nova Badem IB 192, Ouro Preto IB 897, 3311, Passa Vinte IB 4968, Pocos de Caldas IB 4714, Santa Rita de Extrema IB 5560, 8192, Taboleiro Grande ZMUC 601253, Toledo IB 44531, Ubá IB 17308. Paraná: Araucaria IB 7252, 7346, 13632, Balsa Nova IB 18293, 2939–22941, 22943–22944, 23112, 23114–12115,

24343–24345, 24466, 26226, 28785, 32538, Campo Largo AMNH 102257, Carambei IB 7403, Castro IB 6244–6247, 7931, 10392, Curitiba UMMZ 108722, IB 197, 23006, 23439–23440, 29321, Dorizon IB 893, Guarapuava IB 24630, 24661, 24710, 24889, 26954, Jaguaraiava IB 17842, Joaquim Murtinho IB 8263, João Eugenio IB 13027, 15700, Mallet IB 18775, 19544, 19670, Paulo Frontin IB 24986–24987, 25321, Pirai do Sul IB 12425, Rio Azul IB 21346, 22801, Tronco IB 730. *Rio de Janeiro*: Friburgo MZUSP 2705–2707, Muri IB 21261, 21929, 24579, Petropolis IB 21473, 21475, Rio de Janeiro (Morro da Urea) IB 985. *Rio Grande do Sul*: no specific locality. BM 82.10.4.60–82.10.4.61, 61A, MCZ 5633, 17932–17933, MZUSP 1109, 1112–1113, 1127–1128, UMMZ 67241, ZMUC 601254–601255, Alexandrinha MZUSP 5472, Cacequi IB 10025, Canela IB 13526, Caxias do Sul IB 6418, 6716, 9316, Cachoeira do Sul 23315, 23317, Cruz Alta IB 18386, Estação Ecológica do Taim MZUSP 7524, Guaíba CAS 89672, Pareci Novo IB 7645, Passo Fundo IB 8049, 8060, 8212, Pelotas IB 41057, Porto Alegre IB 7264, 7572, 17015, 22411, 22509–22511, 22565, 22832, 23189, 23419–23420, 23543, 45935, Quebra Dente-Maran IB 23302, Restinga Seca IB 7305, 9837, São João MNHP 1894.440, São Leopoldo MSUSP 4100, IB 7300, 7352, 7776, 8357. *Santa Catarina*: Barracas IB 13319, Canoinhas, near Taunay IB 24612, Itaiópolis IB 16669, Lagoa do Norte IB 9700, Porto União IB 25992, São Joaquim IB 45187, Taunay IB 16328, Tres Barras IB 7948. *São Paulo*: no specific locality MCZ 207110–20713, UMMZ 62804, 108760, Agudos IB 22097–22100, Abernethia IB 9553, Altinópolis IB 19562, Araraquara IB 19413, Arpui IB 831, Atibaia IB 23149, 23254, 26889, 26889, Anhanquêra, KM 24 IB 23163, Barrinha IB 43133, Barueri IB 6987, Bento Quirino IB 20641, Boqueirão da Praia Grande IB 11524, Boraceia MZUSP 4498, Botucatu MZUSP 2406, Bragança Paulista IB 30498, Caieiras IB 41061, Caixa D'Água IB 5459, 5682, 6716, Campo Largo 4639, Campo Limpo IB 4738, 5309, 5745, 7349, 7541, 18658, Campos do Jordão IB 8450, 30692, MZUSP 1122, Capituiua IB 3070, Cotia IB 7504–7505, 24281, 29195–29196, Embu km 28, IB 30488, 30490–30494, 305741, Embu Guaçu IB 16617, 167796, 34299, Estação Gabriel Piza IB 5428, Guarulhos IB 5041, 23556, 23724, 42961, MZUSP 4721, Ibiuna IB 26979, 32251, 32265, 40930, 42203, 42222, 42337, 43764, Itapetininga IB 10287–10288, Itapeverica da Serra IB 41115, 42138, 42942, 43882–43883, 44116, 44189, 44498, Itatiba IB 5551, 5586, 5741, 24185–24186, Itaquera IB 10189, 10197–10200, Itu IB 32234, Jacarei IB 3293, 24926, 28502, Jarinu IB 12810, 27542, 30886, Jundiá IB 19686, Lóbo IB 3253, macedonia IB 7026, Mairipora IB 24380, 26949, 27958, Mairinque IB 6042, 6048, 6075, 6618, Mogi das Cruzes IB 10196, 10268, 10295, 10318, 21387, 21395, 22596, Moreiras IB 17606, Pederneras IB 5470, Peruibe IB 5532, Perus IB 3292, Pindamonhangaba IB 18820, Pinheirinhas IB 32420, Pirituba IB 908, Pilar do Sul IB 32121, 32454, Quilãua IB 6257–6258, Raiz da Serra MZUSP 1114–1116, Ribeirão Pires IB 10232, Ribeirão Preto IB 22831, Rodovia Dos Bandeirantes dm 60, IB 34397, Salto IB 4516, 4578–4579, São Bento do Sapucaí IB 3283, São Bernardo do Campo MZUSP 3289, 3682, 4463–4465, IB 22608, 42919, São Lourenço da Serra IB 45789, São Paulo MZUSP 1117, 1119, 1950, 2372, 2387, 2609, 2635, 2960–2961, 3355, 3688, 4095, 4130, 4756, IB 191, 193–95, 647, 695, 1315, 1321–1322, 1416–1417, 3252, 3494, 4643, 5411, 5573, 6189, 7646, 8042, 8575, 9561, 9842, 9879, 10194–10195, 10252, 10271, 12214, 12977, 12986, 17085, 17871, 18270, 18405, 18920, 22882, 24178, 24431, 24442, 26656, 27014, 27157, 27212, 27281, 27478, 27498, 27556, 27571, 27631, 28308, 28503–28508, 29222, 29236–20237, 29249, 29614, 29924, 30683, 32446, 32504, 32800, 32803, 32925, 32999, 34277, 41129, 42109, 42195, 44162, 45746, 45751, São Roque IB 5391, 44228, Serra da Bocaina MZUSP 4912, Sorocaba IB 6865, Souza IB 23151, Sumaré IB 1332, Suzano IB 20376, Tapiraí IB 28060. Tremembé IB 10368, Valentim Gentil IB 28671, Vinhedo IB 30320. URUGUAY. *Canelones*: no specific locality BM 84.2.23.39, FMNH 10215, Arroyo Solis Grande CM 38959, Bañados de Carrasco CM 55422–55423, Rocha USNM 89995, Ruta Interbaleñaria CAS 93100. *Montevideo*: no specific locality MNHP 171, Santiago Vazquez LSUMZ 27753, MNMHP 168.

### *Liophis maryellenae* Dixon

*Liophis maryellenae* Dixon, 1985. Holotype—AMNH 62202. Type-locality—Annapolis, Goiás, Brazil.

*Description.*—The following description is based on 10 specimens. Maximum total length of males 435 mm, of females 530 mm. Tail/total length ratios vary from 0.221 to 0.262 ( $\bar{x}$  = 0.240). Diameter of eye/snout length ratios vary from 0.605 to 0.844 ( $\bar{x}$  = 0.686). Dorsal scale rows are 19–19–17, smooth, with an apical scale pit. Reduction to 17 rows occurs between ventrals 74 and 95 ( $\bar{x}$  = 82.8). The anal plate is divided. The number of ventrals varies from 144 to 159 ( $\bar{x}$  = 150.9). The number of subcaudals varies from 63 to 82 ( $\bar{x}$  = 67.9). The number of maxillary teeth varies from 25 to 28 ( $\bar{x}$  = 26.1). Head scales vary as

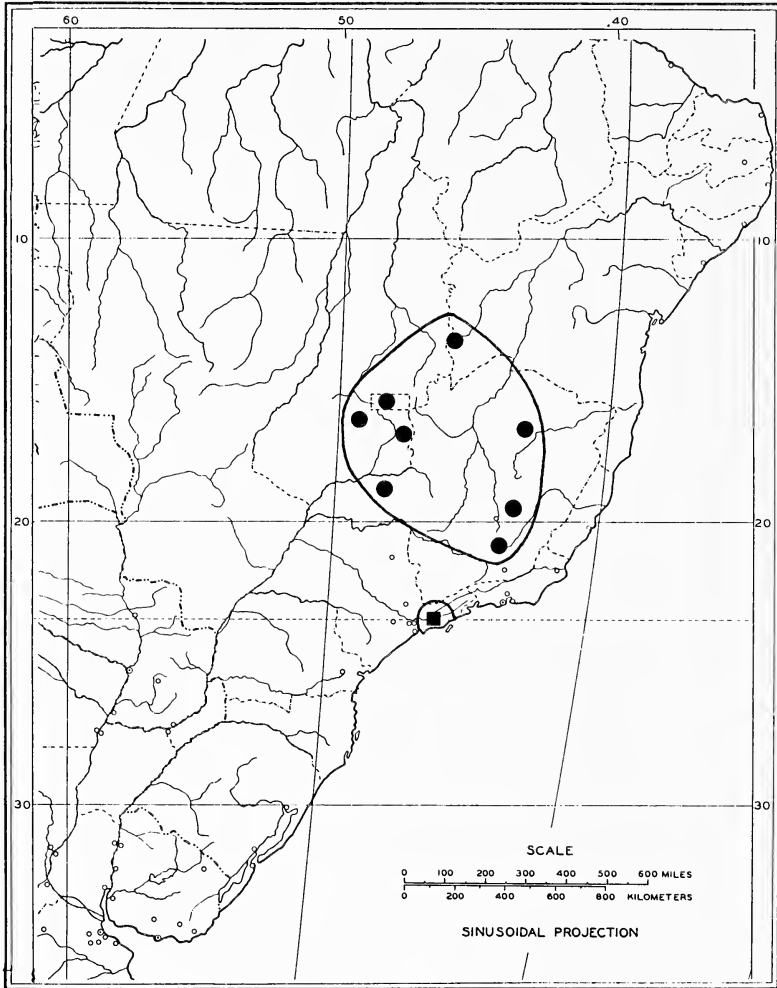


Fig. 4.—Distribution of *Liophis atriventer* and *L. maryellenae* in southeastern Brazil. Dots represent *L. maryellenae*; the square, *L. atriventer*.

follows: supralabials 8-8 (10), supralabials entering orbit 4+5 (10), infralabials 10-10 (8), 11-11 (2); preoculars 1-1 (10); postoculars 2-2 (10); loreals 1-1 (10); temporals 1+2 (10).

The hemipenes vary between (*in situ*) 9.5 to 12 ( $\bar{x}$  = 10.5) subcaudals long. The structure is slightly bilobed, each lobe about two subcaudals in length, and their distal ends have a smooth apical disk. The sulcus spermaticus divides about the middle of the shaft. The entire structure is spinose, with the spine length decreasing gradually from the base to the apex. A basal naked pocket is present.

The dorsum is usually some shade of green, grayish to olive green, with some indication of a brown or reddish brown mid-dorsal stripe. Other dark lines may be present laterally; some indication of dark flecks may occur over the body. In life, the venter is yellowish orange. For more details of color, see Dixon (1985).

*Distribution.*—This species apparently is restricted to the tablelands of southeastern Brazil (Fig. 4). For specimens examined, see Dixon (1985).

*Liophis atriventer* Dixon and Thomas

*Liophis atriventer* Dixon and Thomas, 1985. Holotype—MZUSP 5066. Type-locality—Boraceia (Estação Biológica), São Paulo, Brazil.

**Description.**—the following description is based on three specimens. Maximum total length of male 505 mm in snout–vent length). Tail/total length ratios vary from 0.195 to 0.214 ( $\bar{x}$  = 0.203). Dorsal scales are in 19-19-17 rows, smooth, without apical scale pits. The reduction to 17 rows occurs between ventrals 73 and 79 ( $\bar{x}$  = 76.7). The anal plate is divided. The number of ventrals varies from 141 to 148 ( $\bar{x}$  = 144.0). Number of subcaudals from 49 to 56 ( $\bar{x}$  = 52.5); the number of maxillary teeth from 23 to 24 ( $\bar{x}$  = 23.2). Head scales are as follows: supralabials 8-8 (3), supralabials entering orbit 4+5 (3), infralabials 10-10 (3), preoculars 1-1 (3), postoculars 2-2 (3), temporals 1+2 (3).

The hemipenis of the only known male is short, 5.5 subcaudals long (in situ), and bilobed for the distal half. The sulcus spermaticus divides about one third of the distance from the base. The distal end of the lobes contain smooth apical disks. Five large spines are present along the outer surface of each lobe, near its base, while the inner surface of the lobe is bare. In addition to the larger spines, many smaller ones are scattered over the shaft.

In preservative, the dorsum is uniform olive brown. The throat and first seven ventrals are grayish white, and the remainder become progressively darker until the posterior two-thirds of the venter is black. The subcaudals are grayish with occasional dark smudges.

**Distribution.**—This taxon is known only from the type locality (Fig. 4). See Dixon and Thomas (1985) for specimens examined.

Key to the "Green" *Liophis* of South America

- |   |                    |
|---|--------------------|
| 1. Scale rows 19-19-15 or 19-19-17 .....          | 2                  |
| Scale rows 17-17-17 or 17-17-15 .....             | <i>jaegeri</i>     |
| 2. Scale rows 19-19-15 .....                      | 3                  |
| Scale rows 19-19-17 .....                         | 4                  |
| 3. Ventrals 133–172, one scale pit .....          | <i>typhlus</i>     |
| Ventrals 187–199, no scale pit .....              | <i>guentheri</i>   |
| 4. Ventrals 141–159, maxillary teeth 23–26 .....  | 5                  |
| Ventrals 169–202, maxillary teeth 17–24 .....     | <i>viridis</i>     |
| 5. Subcaudals 62–82, belly yellowish orange ..... | <i>maryellenae</i> |
| Subcaudals 49–56, belly black .....               | <i>atriverter</i>  |

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A NEW SPECIES OF *CLINIDIUM* KIRBY  
(COLEOPTERA: CARABIDAE OR RHYSODIDAE) FROM  
MEXICO, AND DESCRIPTIONS OF THE FEMALES OF  
TWO NEOTROPICAL MEMBERS OF THE GENUS

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ABSTRACT

*Clinidium* (*Mexiclinidium*) *reyesi* is described from Volcán Tacaná in the Sierra Madre de Chiapas in Chiapas State, southern Mexico. It is intermediate between known species of Subgenus *Mexiclinidium* and *Clinidium* (*Protainoa*) *extrarium*, so *Protainoa* is suppressed and *C. extrarium* is included in Subgenus *Mexiclinidium*. Females are also described for *C. (Mexiclinidium) newtoni* Bell and Bell, from the same region, and *C. (sensu stricto) mathani* Grouvelle, from Brazil.

SYSTEMATICS

*Clinidium* (*Mexiclinidium*) *reyesi*, new species

*Type material*. — HOLOTYPE male, labelled "Volcán Tacaná, Talquián, Mpio. Unión Juárez, Edo. de Chiapas, alt. 1940 m, 26-VIII-81, P. Reyes, G. Quintero, M.L.Y.C. Castillo." PARATYPES, 2 females, same place and date, one collected by P. Reyes and J. Valenzuela, the other by P. Reyes and G. Quintero. (All specimens in the Museo de Historia Natural de la Ciudad de México.)

*Description*. — Length 7.0–7.4 mm. Antennae with tufts of minor setae on segments 6–10; basal setae present on segments 8–11; head longer than broad; median lobe relatively long, ending just anterior to posterior margin of compound eye; postorbital, suborbital tubercles absent.

Pronotum relatively short; length/greatest width 1.40; lateral margins curved; apex strongly narrowed; base moderately narrowed; basal impression large, about 0.3 of length of pronotum, open posteriorly; pollinosity continues across anterior margin; inner, outer marginal grooves equally deep, outer one barely visible in dorsal view; angular seta present; precoxal seta absent (Fig. 1).

Intercalary stria ending blindly posteriorly; sutural, parasutural, intercalary, and intratubercular striae deeply impressed, separated by narrow cariniform intervals; female with slight concavity toward apex of intercalary stria (Fig. 2, 3); supra-marginal stria (see Bell and Bell, 1985:6) incomplete, not impressed, represented by row of minute punctures; marginal stria effaced in basal 0.25, remainder impressed, becoming deeper toward apex; sutural stria with 1–2 setae near apex; parasutural without setae; intercalary with 1 seta at apex; intratubercular with 2–3 near apex; marginal with about 4 near apex; transverse sulci of abdominal sterna narrowly interrupted at midline, medial end of each sulcus with enlarged pit; sternum VI with 4–8 very large, irregular punctures (Fig. 4); male with indefinite lateral pit on sternum IV, pollinosity of transverse groove extended slightly into

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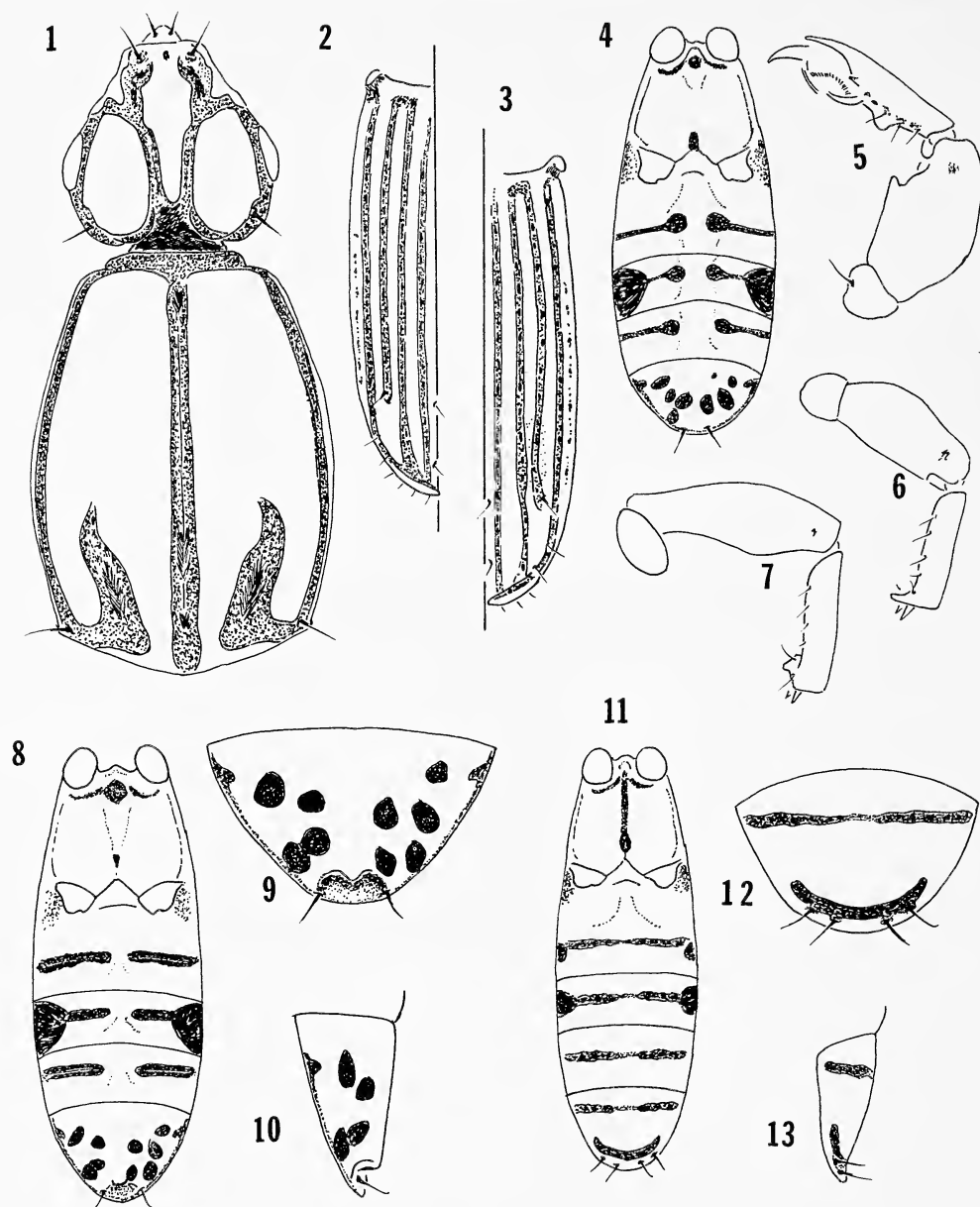


Fig. 1-7.—*Clinidium reyesi* new species. 1. Head and pronotum, dorsal view. 2. Elytron, left half, dorsal view, male. 3. Elytron, right half, dorsal view, female. 4. Metasternum and abdomen, ventral view, female. 5. Anterior leg (excluding tarsus), male. 6. Middle leg (excluding tarsus), male. 7. Hind leg (excluding tarsus), male.

Fig. 8-10.—*Clinidium newtoni* Bell and Bell, female. 8. Metasternum and abdomen, ventral view. 9. Sternum VI, ventral view. 10. Sternum VI, lateral view.

Fig. 11-13.—*Clinidium mathani* Grouvelle, female. 11. Metasternum and abdomen, ventral view. 12. Sternum VI, ventral view. 13. Sternum VI, lateral view.

pit; female with lateral pit of sternum IV enlarged, transverse groove of sternum IV with pollinosity not extending into pit; anterior trochanter of male without tooth; anterior femur of male with large, sharp tooth; anterior tibia of male with proximal tooth (Fig. 5); female without femoral or proximal tibial tooth; middle calcar of male acute (Fig. 6); hind calcar falcate (Fig. 7).

This species differs from all previously described species of *Mexiclinidium* in having a tuft of minor hairs on antennal segment 6. This alone will identify it. In our last key to the subgenus (Bell and Bell, 1985), it would be hard to work through the key, since the position of the marginal grooves of the pronotum, used in couplet 1, is intermediate between 1 and 1'. The enlarged pits at the medial ends of the transverse sulci of the abdomen are similar to those of *C. guatemalenum* Sharp; however the complete strip of pollinosity across the anterior margin of the pronotum, the absence of precoxal setae, and the reduced marginal stria will distinguish the new species.

*Clinidium reyesi* also resembles *C. (Protainoa) extrarium* Bell and Bell, 1985. In fact, the latter appears less isolated than when we created the subgenus for it. We hereby synonymize *Protainoa* and incorporate *C. extrarium* into *Mexiclinidium*. Couplet 2 of the key to subgenera (Bell and Bell, 1985:59) should be altered as follows:

- 2(1) Parasutural stria complete anteriorly; marginal setae of pronotum absent; angular seta present or absent ..... *Mexiclinidium* Bell and Bell
- 2' Parasutural stria restricted to posterior 0.5 to 0.25 of elytron; marginal and angular setae present ..... *Tainoa* Bell and Bell

The description of *Mexiclinidium* should be altered to read "antennae with tufts of minor setae on VII–XI or VI–XI."

The key to species should be altered by the insertion of two couplets at the very beginning, as follows:

- 0.1 Antenna with tufts of minor setae on segments VI–XI ..... 0.2
- 0.1' Antenna with tufts of minor setae on segments VII–XI ..... 1
- 0.2(0.1) Intercalary stria ending blindly posteriorly; pronotum with two complete marginal grooves; basal impressions open posteriorly; hind angle of pronotum obtuse ..... *C. reyesi* new species
- 0.2' Intercalary stria complete; pronotum with 1 marginal groove which is effaced posteriorly; basal impressions closed posteriorly; hind angle of pronotum denticulate ..... *C. extrarium* Bell and Bell

#### *Clinidium (Mexiclinidium) newtoni* Bell and Bell 1985

*Description of female.*—Similar to male, except that calcars are lacking, anterior trochanter and femur not dentate; transverse sulci of abdomen very narrowly interrupted at midline, midline smooth, shining; sulcus of sternum IV forming large glabrous lateral pit (Fig. 8); sternum VI impressed near tip, in some specimens forming small median tubercle (Fig. 9, 10). (In male, sulci slightly more separated, area between finely microsculptured.)

We have studied the following additional specimens of *C. newtoni*: 4 males, 3 females, from Mexico: Chiapas State, Municipio Angel Albino Carzo, Camino al Triunfo, alt. 1410–1880 m, several dates and collectors, April and August, 1983 (all in the Museo de Historia Natural de la Ciudad de México). They vary in length from 7.0–8.5 mm.

***Clinidium (sensu stricto) mathani* Grouvelle**

*Description of female.*—Length 7.5 mm. Similar to male in most respects, but without calcars; small lateral pit present on sternum IV, only slightly more developed than in male; very small lateral pit on sternum III (Fig. 11–13).

We have studied one specimen labelled “Brasil: Amapá, Porto Platon, IX-1957, K. Lenko” (The Carnegie Museum of Natural History).

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BIOSYSTEMATIC STUDIES IN *STENANTHIUM*  
(LILIACEAE: VERATREAE) II. FLORAL MORPHOLOGY,  
FLORAL VASCULAR ANATOMY, GEOGRAPHY AND  
TAXONOMY OF THE MEXICAN *S. FRIGIDUM*  
(SCHLECHT. & CHAM.) KUNTH

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ABSTRACT

The floral morphology, continuous pedicel to stigma floral vascularization, distribution and taxonomy of *Stenanthium frigidum*, a bulbous lily confined to the Trans-Mexican Volcanic Belt, are presented. The perfect, protandrous flowers with bilobed or v-shaped tepal nectaries are arranged in andromonoecious panicles. Raphide idioblasts were observed in the upper gynoecium and recurved stylar arms. Total floral vascularization is derived from three, compound, lower pedicel bundles. Both outer and inner tepallary and staminal bundles as well as dorsal vasculature are formed above the level at which the ventrals and ovular supplies are established due to an inferior gynoecium with a central capillary hole and epigynous perianth. Within each septal arm, a pair of septal laterals fuse with a pair of ventrals from which they had a common origin. As these septal laterals re-associate with the ventrals, septal indentations occur. The bitegmic, camplyotropous ovules develop into flat, winged seeds.

INTRODUCTION

Four *Stenanthium* species are currently recognized: *S. occidentale* (western North America), *S. gramineum* (eastern North America), *S. sachalinense* (eastern Asia) and *S. frigidum* (central Mexico). Of these, the tall, showy, purplish-black flowered *S. frigidum* (Schlecht. & Cham.) Kunth has the most southern distribution, along with representatives of *Schoenocaulon* (= *Sabadilla*), of the wide-ranging, northern hemispheric Veratreae (Baker, 1879; Engler, 1889; Krause, 1930; Zimmerman, 1958; Melchior, 1964; Hutchinson, 1973) with nearly 80 species world-wide (Dahlgren et al., 1985).

Though poisonous alkaloids are commonly known in the Veratreae (Kupchan et al., 1961; Williaman and Schubert, 1961; Hegnauer, 1963), the only notes concerning such occurrences in *S. frigidum* are "that natives of Mount Orizaba know it to be dangerous to the horses that bite it" (Schiede, 1829), "folia pecoribus lethalia" (Bentham, 1839) and "it may be supposed to furnish a part of the venomous sabadilla seeds of commerce, from which veratria is prepared" (Lindley, 1846). Several common names have been used—"sevoeja" (Schiede, 1829; Lindley, 1849a), "cebadilla de tierra fria" (Lindley, 1849b), "cebolleta" (Hinton 4612 MO), "cebolleja" (Balls 4886 UC), "flores angostas" (Conzatti, 1947) and "cebadilla" (Sanchez, 1980). During the Mexican botanical exploration of the middle of the last century, the same illustration was used three times by Lindley (1846, 1849a, 1849b) to promote the plant's economic and horticultural value. The species has been figured recently in Sanchez (1980). Chromosome counts are unknown for the species.

This second paper in a series on the genus *Stenanthium* (Utech, 1987) reports

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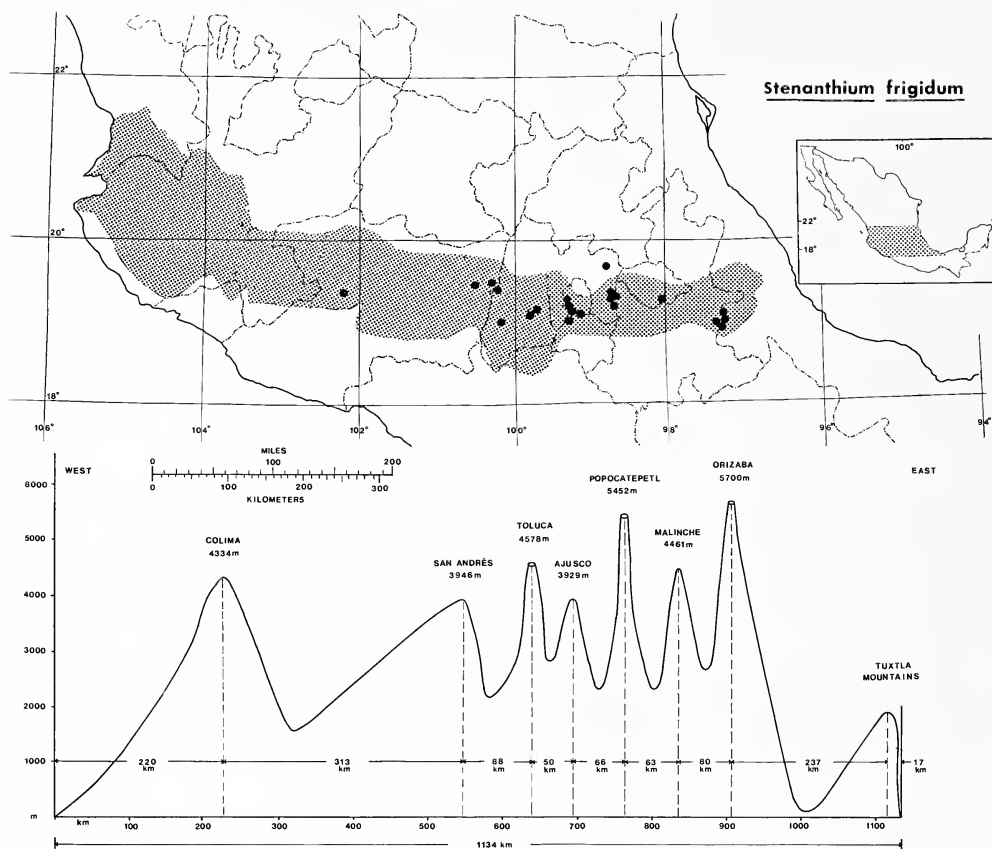


Fig. 1.—Herbarium specimen distribution of *S. frigidum* in the Trans-Mexican Volcanic Belt (Eje Volcánico Transversal) (shaded area). The projection which summarizes the maximum elevation between 18° and 22°N latitude is based in part on Clausen (1959).

on the Mexican species, *S. frigidum*, with emphasis on the inflorescence, flower and the origins of the tepallary, staminal and dorsal bundles for comparisons within the genus and the tribe Veratreae.

## MATERIALS AND METHODS

Floral material of *Stenanthium frigidum* fixed in FAA from Monte Rio Frio pass near Llano Grande, Mexico, was made available for this study by Dr. Hugh H. Iltis, University of Wisconsin–Madison (Iltis *et al.* 1085). Samples for standardized transverse (15) and longitudinal (5) paraffin sectioning (14–16  $\mu$ ) of complete flowers of varying ages were stained in safranin-methylene blue (Johansen, 1940; Sass, 1958). Whole flowers were also cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963) as a check on the prepared sections. Vascular description, presentation and bundle coding follow Utech (1987). Herbarium collections used for distribution (Fig. 1) and floral morphometrics (Fig. 3) are cited in the taxonomic review.

## OBSERVATIONS

**General morphology.**—*Stenanthium frigidum*, a robust, glabrous perennial herb, (4.5) 6.0–11.0 (15.0) dm tall, occurs in scattered clumps from large, 8.5–10.5 cm long by 3.5–5.5 cm wide, bulbs which are covered by a dense, coarse brown tunica.





Fig. 2.—Flowering habit of *S. frigidum*. A. Bracteated panicle with flowers in bud. The progressive reduction in the elongate bracts which subtends the lateral branches is evident. B. Panicle at anthesis showing several nodding terminal segments in which each flower is subtended by a bract as well as the lateral branches. Each flower within a lateral branch is subtended by a bracteole. (Photos A and B from negatives 163 and 159 respectively, courtesy WIS herbarium and vouchered by *Ilitis et al.* 902.)

The 35–60 cm long by 1.0–1.5 cm wide, linear, bifacial, basal leaves are sheathing at their bases and gradually narrowed at both ends. The abaxial surfaces have anomocytic stomatal patterns which are generally lacking on the adaxial surfaces. The fusiform epidermal cells are six-sided. The few stem leaves are progressively reduced apically and intergrade into bracts (Fig. 2).

The simple, andromonoecious panicle occupies the upper 35–45% of the plant's height. Within the panicle, the (35) 45–75 (85) bisexual flowers are distributed over (3) 5–14 nodding lateral branches (racemes) and a dominant terminal segment (Fig. 3). Each branch is subtended by a bract. The lower bracts are always longer than the upper. Within each branch, each flower's pedicel is subtended by a scarious, linear bracteole. The lowest bracteole on a branch, like the lower bracts on the main axis, is always larger. Each of the (10) 15–25 flowers on the dominant terminal segment is subtended by a bract. Flowering begins at the base of the inflorescence and proceeds outwards in the lateral branches and upwards in the terminal segment. Maximum anthesis is between July and August.

*Floral morphology.*—The pendulous, deep fuscous brown to dark blackish maroon flowers on short, glabrous pedicels have long, narrowly acuminate tepals. The bases of the three outer tepals are wider than the inner tepals, though their lengths, 13–16 mm, are similar (Fig. 3). Adaxial, v-shaped tepal nectaries occur basally in both outer and inner tepals (Fig. 8C, D). At anthesis the flowers have

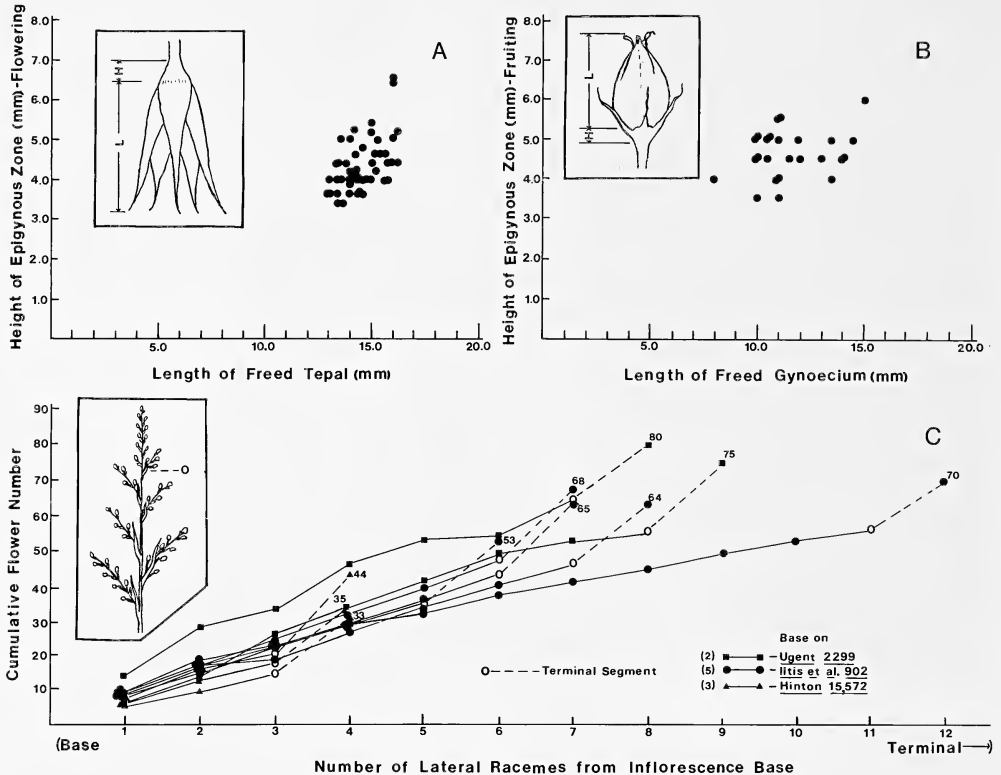


Fig. 3.—Floral and inflorescence patterns in *S. frigidum*. A. Comparison between the length (L) of freed tepals to height (H) of the flowering epigynous zone (mm). B. Comparison between the length (L) of the freed gynoecium (mm) to height (H) of the epigynous zone (mm). C. Inflorescence comparisons showing the total number of flowers and the degree of branching within the panicle. The connecting line indicates the cumulative flower number from one branched increment to the next with the terminal segment marked with an open circle.

a campanulate shape due to tepal spreading from the epigynous zone, but the tips are never reflexed. The six, subulate, glabrous filaments are 3.3–3.6 mm long, with little length differences between the outer and inner sets. The basifixed, extrorse anthers have a valvular dehiscence between the confluent thecae that opens into a reniform, peltate disc. Protandry occurs in *S. frigidum*, since both outer and inner anthers dehisce at the same time, and this is earlier than gynoecial maturity. The free styles and upper areas of the tri-carpellate gynoecium surpass the anther zone at maturity. The pedicels of the fruiting septicidal capsules are erect and elongated compared to anthesis. The ovoid capsules with persistent, withered tepals are 13.5–16.5 cm long and contain numerous winged seeds.

**Floral vascular anatomy.**—Pedicel vascularization: In transverse section, the flowering pedicels above their subtending bracts (bracteoles) are circular and have three large, centrally arranged bundles. Frequently several phloem caps per bundle are observed, attesting to the compound nature of these bundles. It is from these three bundles that the complete floral vasculature is established. The centers of these bundles are located on radii 120° apart and are designated the outer tepal radii.

Near the pedicel's mid-length, each of the three outer tepal radii bundles under-

goes a tri-partite radial subdivision, which results in three bundles. These divisions are not co-planar, but occur at different levels in a spiral pattern. Gaps along the outer tepal radii are created by the outward departure of the central bundle products from each of the three, tri-partite divisions (Fig. 4A). These departing bundles with normally arranged xylem (adaxial) and phloem (abaxial) remain free of other vasculature and establish the outer tepal medians (OTM). At this level, the pedicels have a triangular shape in transverse section with the corners on the outer tepal radii (Fig. 4B).

Immediately following the OTM bundle formation the two adjacent parental bundles undergo additional radial divisions. The two products closest to the gap depart outward with the OTM. There are three such sets of three bundles which correspond to the dorsal-composite bundle of Sterling (1982), and eventually establish the outer tepallary laterals (OTL), staminal (OS) and dorsal (D) vasculature (Fig. 4B–D).

The two remaining lateral products adjoining a gap following the radial divisions fuse with similar adjacent laterals along the inner tepal radii, which are located halfway between the outer tepal radii (Fig. 4B–D). These fusion bundles are formed at progressively higher levels in a spiral pattern. Each of these three, fusion bundles undergoes a tri-partite subdivision and radial division similar to that observed at a lower level among the three original bundles. The central bundle products of this second series of divisions depart along the inner tepal radii and become the inner tepal medians (ITM). The ITM and the two radial division products which depart with the ITM correspond to the “zwischenbündel” of Sterling (1982) and eventually establish the inner tepallary laterals (ITL) and staminal (IS) vasculature (Fig. 4D, E).

Six sets of three bundles each remain in peripheral positions until the upper epigynous zone. Tepallary, staminal and dorsal vasculature formation will be discussed later in a separate section.

**Ventral vascularization:** Following the formation and departure of the inner tepal medians (ITM) and associated lateral pairs, three bundle pairs remain along the inner tepal radii in the central area. It is from these bundle pairs that the complete ventral supply is established (Fig. 4C–F, 6A, B, 8A, B).

An inward rotation towards the inner tepal radii among the central bundle pairs occurs as well as a radial subdivision among these remaining bundles. As the locules open, the six inner most division products with reversed conducting elements depart inwards as a pair to establish the ventrals (V) (Fig. 4D, E, 5A, B). In the epigynous zone, two such ventrals (V) are associated with each locule. The remaining parental products may fuse along the inner tepal radii in a septal axial position. These bundles also divide if they fused and their resulting products have conducting elements which are reversed. There are three pairs of such bundles that could be called septal laterals (L) (Fig. 4E, F, 5A–C). They move inward following the same course as the ventrals. A given septal lateral (L) is re-associated with the same ventral (V) of common origin in the inner septal margins. Ovule supply occurs initially from the ventral (V) bundles in the lower epigynous zone, but in the upper freed gynoecium, the ventrals and laterals which fused in the ventral position continue to supply ovules. These continuing ventrals pass into the stylar region without fusion to other ventrals or dorsals. Four rows of 16–24, bitegmic, campylotropous ovules are associated with each carpel. Ovule supply occurs in the lower epigynous zone below the level of dorsal formation. Raphide idioblasts are common in the upper gynoecium and the free spreading stylar arms.

As the locules open perpendicular to the outer tepal radii in a spiral pattern,

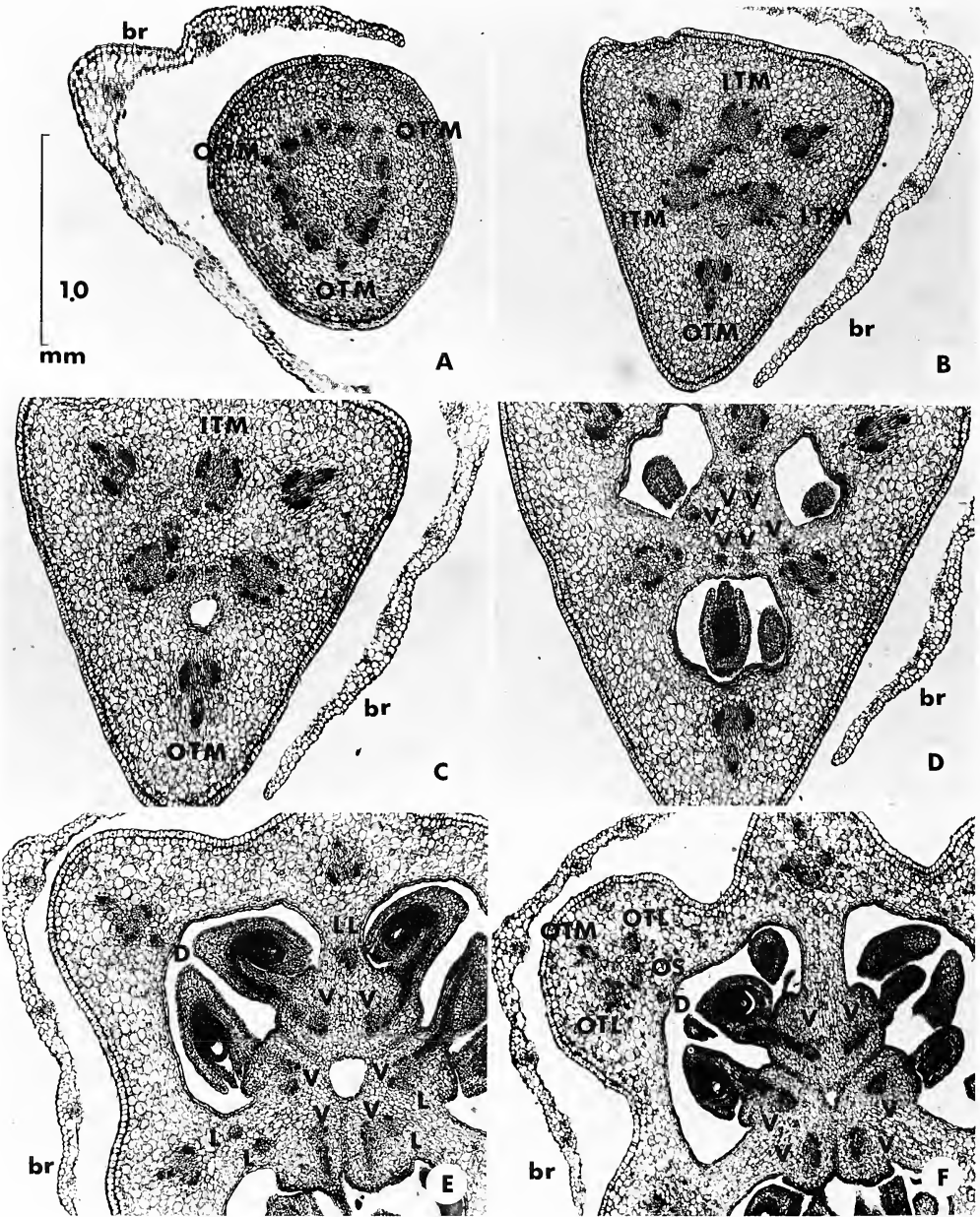


Fig. 4.—Photomicrographs of transverse sections from pedicel to mid-epigynous zone in *S. frigidum*. A. Lower pedicel (circular outline) and subtending bract (br). Three outer tepal medians (OTM) are established at this level. B. Upper pedicel (triangular outline) showing laterals pairs associated with each OTM and the formation of the ITM bundles and their associated lateral pairs. C. Lower epigynous zone showing one open locule and further formation of the ITM bundles, their lateral pairs and ventrals. D. Epigynous gynoecium with three open locules with two ventrals (V) each and the formation of septal laterals. Dorsals are not present at this level. E. Gynoecium with central carpellary hole, inner septal margins subdivided along the inner tepal radii, ovule placentation, septal lateral (L) pairs in the septal arms and dorsal (D) bundles. Outer stamen bundles are not present at this level. F. Re-association of ventrals (V) and laterals (L) in the septal margins. Outer stamen (OS) bundles present.

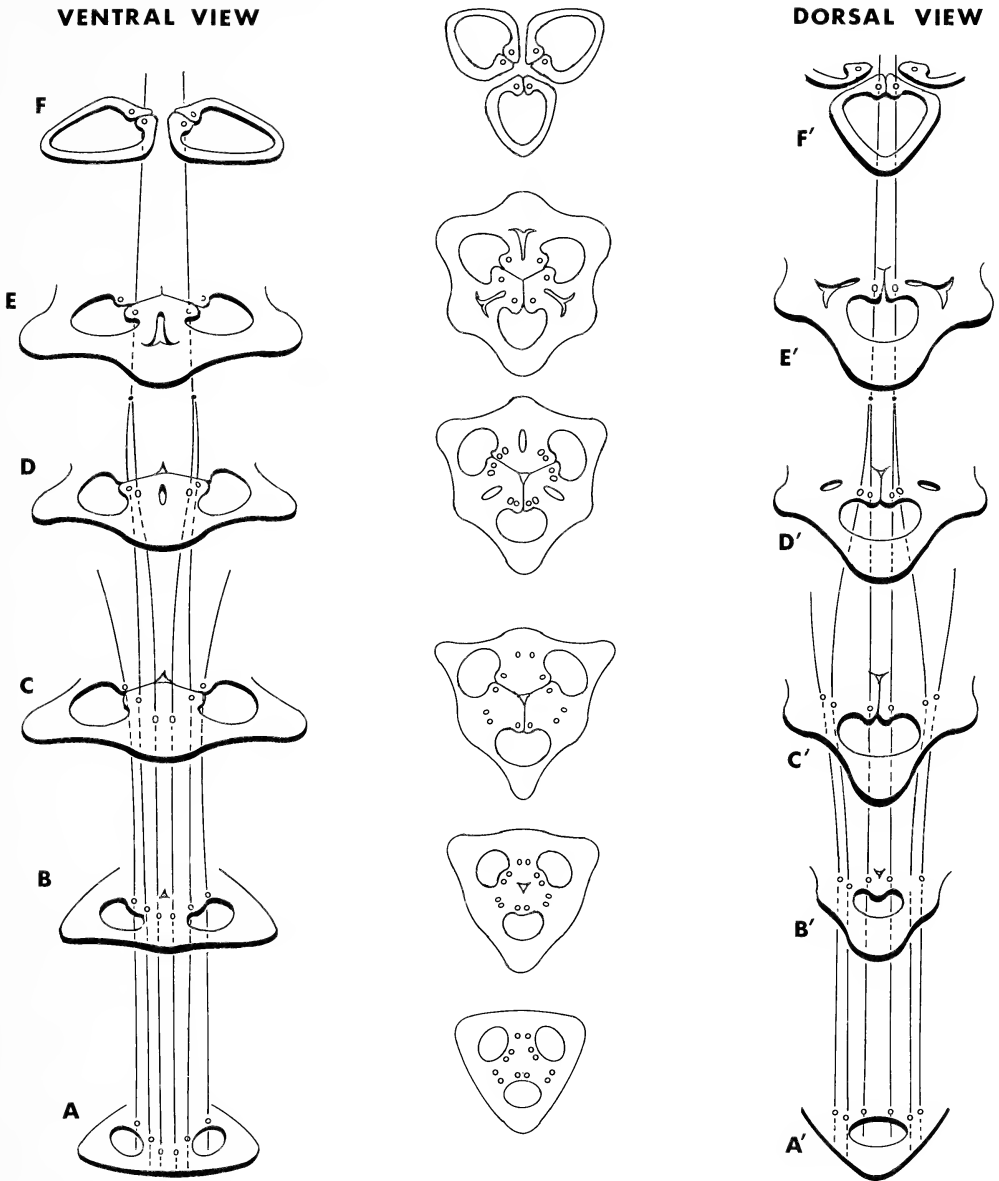


Fig. 5.—Matched ventral (A–F) and dorsal (A'–F') projections of the same section (central column) showing the ventral vascular supply in *S. frigidum*. The ventral projection is along the IS radii, the dorsal along the OS radii. Views A–E are through the epigynous zone, while F is from the freed carpellary zone. View B shows the central carpellary hole, C the subdivided inner septal margins and inter-locular connections, and D the septal indentations within the septal arms.

three septal arms are established within the lower epigynous zone. A central carpellary hole or opening (Fig. 4D–F, 5B), which is continuous with the open stylar canal, appears in the central area before this region is subdivided along the outer tepal radii. This central subdivision creates three inner septal margins or

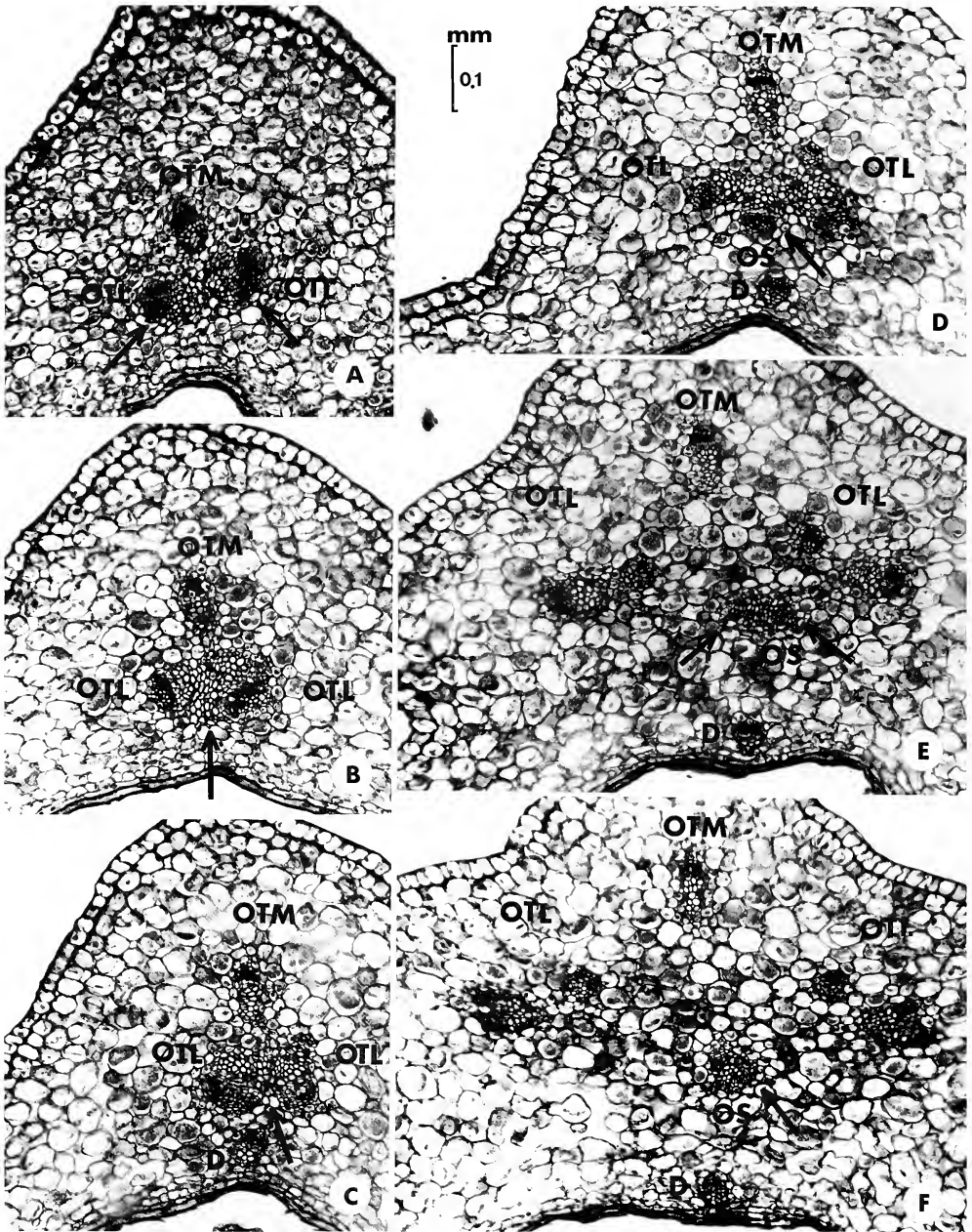


Fig. 6.—Transverse sections through the outer epigynous zone of *S. frigidum* showing the origin of outer tepal, stamen and dorsal vasculature (dorsal-composite bundle). A. Section showing an outer tepal median (OTM) in a distal position and two adjoining, outer tepal laterals (OTL) with laterally orientated phloem caps (arrows). B. Section above A showing xylary fusion and plexus formation between two laterals (OTL). C. Section above B showing a free dorsal with normally arranged conducting elements which was derived from the fusion plexus and the formation of an outer stamen (OS) bundle (arrow). D. Section above C showing an OS bundle (arrow) with reversed conducting elements. E. Section above D showing the outward departure and division of the outer tepal laterals (OTL) and an OS bundle with two lateral phloem caps (arrows). The OTM and D bundles are correctly



wing tips. As the ventral and lateral bundles re-associate in the inner septal margins, septal indentations or slits open within the septal arms along the inner tepal radii. These indentations occur within the upper epigynous zone, and furthermore, are continuous with the zones which separate the gynoecium from the surrounding stamens and tepals (Fig. 5D–F, 8A–C). The three free carpels are only weakly appressed along the central floral axis.

**Tepallary, staminal and dorsal vascularization:** Established in the lower pedicel, the three OTM bundles and their pair of associated laterals plus the three ITM bundles and their lateral pairs have remained in a peripheral position through the epigynous zone. The OTM and ITM medians which are along the outer and inner tepal radii, respectively, are not involved in any further division or fusion. Fig. 6 details the origin of the outer tepal laterals (OTL), outer stamen (OS) and dorsal (D) bundles, while Fig. 7 presents the similar, but less complex pattern for the inner tepal laterals (ITL) and inner stamen (IS) bundles.

From the three bundles in an outer group, the two laterals or the pair associated with an OTM undergo an inward rotation and fusion along the outer tepal radii. From this outer vascular plexus and subsequent subdivision, a dorsal (D) with normally arranged conducting elements results. This is followed by an outer stamen (OS) bundle with reversed conducting elements that shifts to a normal arrangement in the upper epigynous zone. It should also be noted that the dorsals are formed before the outer stamen bundles. The dorsals follow an undivided and unfused course into the upper stylar arms.

The remaining parental laterals depart as the outer tepal laterals (OTL) flanking the OTM. The laterals undergo additional radial divisions such that when the tepal is freed from the epigynous zone, each outer tepal has as many as seven bundles, that is, three OTL + one OTM + three OTL. Additional divisions occur in the freed outer tepal, such that a maximum of 11 bundles can be observed—five OTL + one OTM + five OTL. All of these bundles were established from three at a lower level. There is no terminal fusion between any of the laterals or medians and all end in the upper tepal margins.

The formation of inner tepal lateral (ITL) and stamen (IS) bundles parallels that for the OTL and OS bundles, except no dorsal is associated with the inner members. At the base of each freed inner tepal, a seven bundled condition exists, that is a median (ITM) and two sets of three laterals (ITL). The freed inner tepals, like the outer tepals, can have a maximum of 11 bundles, that is five ITL + one ITM + five ITL, which were derived from three lower bundles.

Each of the six stamens receives a single bundle or staminal trace. Epitopally occurs in both the outer and inner stamens.

*Geography and taxonomy.*—*Stenanthium frigidum* occurs in a most specialized ecological zone—the Trans-Mexican Volcanic Belt (Clausen, 1959) or “Eje Volcanico Transversal” (Rzedowski, 1978) (Fig. 1). Scattered clumps are frequently encountered in open, rocky, grassy, alpine meadows associated with *Pinus hartwegii* forests (Beaman, 1962, 1965) between 18° to 22°N latitude at an elevation of 9000–12,000 ft (ca. 2700–3700 m). *Stenanthium frigidum* was first described by Schlechtendal and Chamisso (1831) as *Veratrum frigidum* from a C. J. W.

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positioned. F. Section above E showing a normal element arrangement for the OS bundle (arrow) and further outward departure of the laterals (OTL).

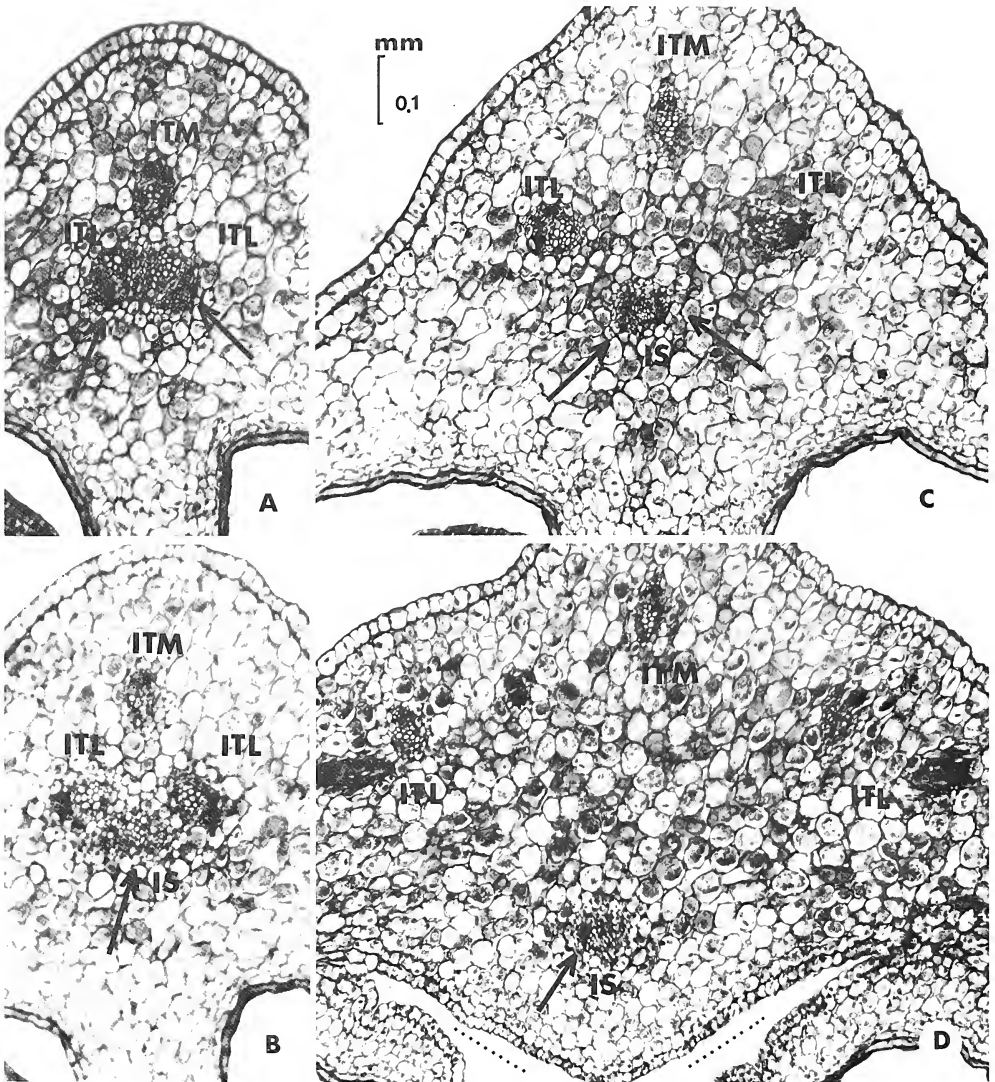


Fig. 7.—Transverse sections through the outer epigynous zone of *S. frigidum* showing the origin of inner tepal and stamen vasculature (zwischenbündel). A. Section showing an inner tepal median (ITM) in a distal position and two inner tepal laterals (ITL) with laterally oriented phloem caps (arrows). Fusion has occurred between the xylar elements. B. Section above A showing laterals (ITL) departing and an inner stamen (IS) bundle with reversed conducting elements (arrow). C. Section above B showing an inner stamen (IS) bundle with two lateral phloem caps (arrows). D. Section above C showing normal element arrangement of the IS bundle and division of both inner tepal laterals (ITL), and the carpellary wall separated from the epitepalous stamen (dotted lines).

Schiede and F. Deppe collection from the alpine regions of Mt. Orizaba (Fig. 9). Schiede and Deppe left Bordeaux in May 1828, arrived at Veracruz in July 1828 and began collecting in the Jalapa and Orizaba areas (Schiede, 1829). Their collections, including type material, are known from the following herbaria (Holmgren et al., 1981): “B (original set destroyed; set *ex* herbarium Baschant extant),



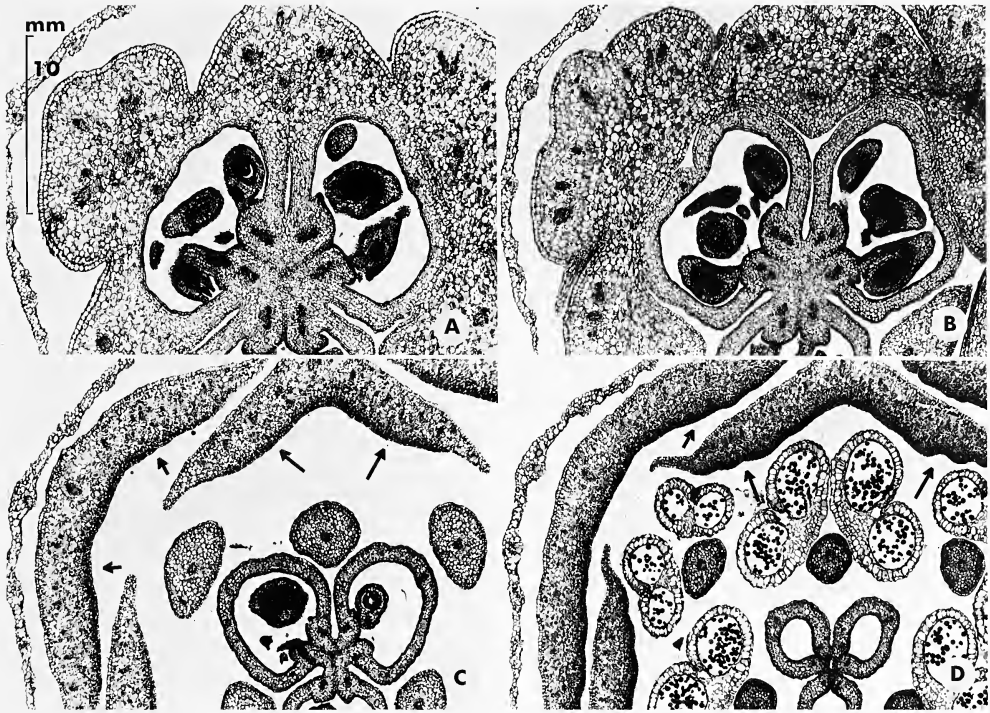


Fig. 8.—Photomicrographs of transverse sections from the upper epigynous zone to the upper floral zone in *S. frigidum*. A. Upper epigynous zone showing the septal indentations along the inner tepal radii within the septal arms. Tepallary and staminal bundles established. B. Separation of gynoecium from surrounding stamens and tepals. Epitopally among both the outer and inner stamens and the formation of additional tepal laterals (OTL and ITL) evident. C. Adaxial surface of freed tepals nectiferous (arrows). Outer (OS) and inner (IS) filaments with a single bundle evident. D. Adaxial tepal nectaries (arrows) at the same level as the reniform, peltate anthers. The adaxial nectiferous surface at higher levels occurs marginally, thus creating a basal V-shaped nectary.

HAL (sent to Schlechtendal); further material BM, BR, C, CGE, F, FI, G, GH, GOET, K, KIEL, LE, LZ (destroyed), M, MO, OXF, P, S, U, US, W, XAL (photos)” (Stafleu and Cowan, 1985). Type material exists for *S. frigidum* (Fig. 9) and it is very probable that additional material is available for lectotypification. Subsequent taxonomic reviews have placed this species in *Zigadenus* (Don, 1832), *Asagraea* (Lyons, 1907) and *Stenanthella* (Gates, 1918). The transfer to *Stenanthium* was made in 1842 by Kunth.

### *Stenanthium frigidum* (Schlechtendal & Chamisso) Kunth

*Stenanthium frigidum* (Schlechtendal & Chamisso) Kunth, Enum. Plant., 4:190–191. 1842.

*Type*.—Mexico, Veracruz, Mt. Orizaba, alpine region, 1831, *Schiede & Deppe* 983 (MO!; fragment GH!; Photos CM)—Fig. 9.

*Veratrum frigidum* Schlecht. & Cham., Linnaea, 6:46. 1831.

*Zigadenus frigidus* (Schlecht. & Cham.) D. Don, Edinb. New Phil. J., 233. 1832.

*Asagraea frigida* (Schlecht. & Cham.) Lyons, Pl. Names Scientif. Pop., 2nd ed., 508. 1907.

*Stenanthella frigida* (Schlecht. & Cham.) Gates, J. Linn. Soc., London, Bot., 44:152. 1918.

*Representative specimens examined*.—MEXICO: DISTRITO FEDERAL: Cima station, hills, 9800 ft, 30 AUG 1905, *Pringle* 13,622 (CAS, GH, LL, TEX, US); Ajusco, Morelos, 3000–3700 m, SEP



Fig. 9.—Type of *S. frigidum* from Mt. Orizaba, Mexico, collected in 1828 by Schiede and Deppe (1883). The MO specimen is from the Bernhardt herbarium. (Courtesy of Missouri Botanical Garden.)

1925, *Lyonnet* 22 (GH, MO, NY, US); Mt. Gauzin (Guauhtzin), between rocks in alpine meadow, 10,900 ft, 26 AUG 1928, *Antipovitch* 96 (CM); La Portrera, 9000 ft, 22 AUG–19 SEP 1930, *Russell & Souviron* 150 (US); S slope of Serjana de Ajusco, ca ¼ km E of Zampoalo on road to Huitzilac, 3000 m, 15 JUL 1960, *Iltis, Koepfen & Iltis* 253 (WIS); 2 km N of La Cima, SE slope of Cerro Pelado, 1–2 km N and W of La Cima station, 3050–3300 m, 14 AUG 1960, *Iltis, Koepfen, Iltis & Rzedowski* 902 (UC, WIS—8 sheets); Cerro de San Miquel, near summit in grassy area, 31 JUL 1960, *Penalosa* 813 (CAS); Cerro Pelado, Serrania del Ajusca, 3100 m, 14 AUG 1960, *Rzedowski* 12,630 (MSC). **MEXICO:** Zinanteatl Mts., moister places of pine forests of Nevado de Toluca, 12,000 ft, 2 SEP 1892, *Pringle* 4257 (GH, MO, NY, UC, US); Ixtaccihuatl, meadows near timber line, NOV 1905, *Purpus* 1699 (GH, NY, UC, US); Temascaltepec, Cajones, 2480 m, 11 NOV 1932, *Hinton* 2396 (GH), *Crucero Aqua Blanca*, 3170 m, 29 AUG 1933, *Hinton* 4612 (CAS, MO); Cierrita, 13 AUG 1935, *Hinton* 8353 (GH, NY, UC, US); pine forest, 18 DEC 1935, *Hinton* 8792 (GH, LL, NY, UC, US); Apitza, Mt. Ixtaccihuatl, 12,000 ft, said by natives to be poison to animals, 27 JUL 1938, *Balls* 5136 (UC, US); Valle de Mexico, C. de Llano Grande, 2800 m, 30 JUL 1950, *Matuda* 19,002 (UC); Ixtaccihuatl, 3500 m, 7 JUN 1953, *Matuda* 28,389 (UNC); Telapon, N of Ixtaccihuatl, 3450–3500 m, grassy meadow under *Pinus hartwegii* forest, 4 SEP 1958, *Beaman* 2443 (GH); Ascenso al Nevado de Toluca, en bosque de *P. hartwegii*, 3789 m, 5 SEP 1958, *Hernandez s.n.* (CAS); S of Pan-Am highway at pass of Monte Rio Frio (5 km WNW of Rio Frio) at Llano Grande, 3100–3200 m, 18 AUG 1960, *Iltis, Koepfen & Iltis* 1085 (UC, WIS—4 sheets); 3100–3200 m, 24 SEP 1962, *Ugent* 2299 (WIS—14 sheets); Papayotl (El Papayo), 2 OCT 1966, *Boege* 292 (CAS); Ixtapaluca, Estacion Experimental de Investigacion y Ensenanza de Zoquiapan, 8 km S de Rio Frio, 3190 m, 5 SEP 1975, *Koch & Magana* 75,496 (CAS, F, NY); sotobosque de *Pinus hartwegii*, 3300 m, JUL 1976, *Obieta* 75 (CAS); Ixtapaluca, Llano de San Miquel, 3350 m, 26 AUG 1978, *Garcia s.n.* (TEX). **MICHOACAN:** Mt. Tancitaro, 10,000 ft, rocky ridge in open pine forest, 4th Hoogstraal Biological Expedition, 22 JUL 1941, *Leavenworth & Hoogstraal* 1135 (GH, MO, NY); Zitacuaro-Cerro Pelon, 3600 m, 14 AUG 1938, *Hinton* 13,238 (GH, LL, NY, UC, US); Vicinity of Morelia, Cerros San Miquel, 2200 m, SEP 1910, *Arsene* 5249 (GH, MO, NY, US); Uruapan, Tancitaro, 3450 m, llano in pine forest, flower and root smell like fungus, said to poison cattle, 23 OCT 1940, *Hinton* 15,572 (GH, LL, MO, NY, TEX). **PUEBLA:** Lower slopes of Pico de Orizaba, W of Chalachicomula (Ciudad Serdan), 21 SEP 1957, *Beaman* 1788 (GH). **TLAXLALA:** Mt. Malinche, pine woods, 12,000 ft, 22 JUN 1938, *Balls* 4886 (UC, US); N side Mt. Malinche, in open grassy *Pinus hartwegii* forest, 3770 m, 10 AUG 1958, *Beaman* 2244 (GH). **VERACRUZ:** Mt. Orizaba, 12,000 ft, foliage poisonous to cattle and horses, 6 AUG 1891, *Seaton* 203 (GH, NY); Vaquena del Jacal, 10,000 ft, 1841–43, *Liebmann* 14,681 (US); Mt. Orizaba, 10,000 ft, 1841–43, *Liebmann* 14,682 (GH, UC), 14,683 (GH, MO); 25–26 JUL 1901, *Rose & Hay* 5748 (US); Vertiente del Volcan Pico de Orizaba, 3600 m, 27 JUL 1971, *Nevling & Gomez-Pompa* 2071 (GH, NY).

## DISCUSSION

The tall and robust *Stenanthium frigidum* occupies a most unusual geographic and ecological zone, in that it occurs between 9000–12,000 ft in the *Pinus hartwegii* forest of the Trans-Mexican Volcanic Belt and is the southern most and highest occurring member of the tribe Veratreae. The highest elevations attained by *S. occidentale* are near 7500 ft in the Pacific Northwest (Utech, 1987). Numerous other differences also occur between *S. frigidum* and *S. occidentale*.

The branched andromonoecious, bracteated panicle of *S. frigidum* has numerous bisexual, protandrous flowers, in marked contrast to the simple raceme of *S. occidentale* (Utech, 1987) and the highly branched, bracteated panicle of *S. gramineum*. Bracteoles, though small, are present in *S. gramineum*, although Gates (1918) reported their absence. An inflorescence parallel in both *S. gramineum* and *S. frigidum* needs further investigation. Both species have extremes in panicle patterns: one type is lax, open and the other is tight, more compact. The flowers of *S. occidentale* (Utech, 1987) and *S. frigidum* have a characteristic nodding appearance, while in fruit their capsules are erect. A sclerenchymatous sheath surrounds the fruiting pedicel bundles in *S. occidentale* (Utech, 1987), and this also appears true of the erect pedicels in *S. frigidum* based on dried fruiting material.

The dark maroon to purplish-black tepals of *S. frigidum* are not suffused with greenish yellow as in *S. occidentale*, which gives the flowers of the latter a bronze cast. The freed tepals in *S. frigidum* average 14.5 mm in length and appear longer than those of *S. occidentale* (Utech, 1987). This difference is only apparent, since the tepals in *S. frigidum* are not reflexed and those in *S. occidentale* are. Epitepally and similar basal, v-shaped, adaxial, tepal nectaries are found in both species.

Both species have epigynous gynoecium, but their flowering and fruiting proportions differ. In *S. frigidum*, there is little difference in epigynous zone height, which averages 4.3 mm in flower and 4.6 mm in fruit. This zone nearly doubles in *S. occidentale* from a flowering height of 2.3 mm to 4.0 mm in fruit (Utech, 1987). The mature septicidal capsules also differ in shape. In *S. occidentale*, they are rather narrowly elongated to a tapering apex of ascending styler arms, whereas in *S. frigidum* they are more ovoid apically with recurved styler arms. In fruit, the epigynous zone of *S. frigidum* accounts for 28.5% of the capsule's length, while in *S. occidentale*, the same zone averages 16.5%.

The general floral and carpel morphology as well as the basic floral vascular anatomy of *S. frigidum* are similar to that reported for various species within the tribe Veratreae (Anderson, 1940; El-Hamidi, 1952; Ambrose, 1975, 1980; Sterling, 1982; Utech, 1986, 1987). However, there are some specific differences between *S. frigidum* and *S. occidentale* (Utech, 1987). The septal indentations within the septal arms of the upper epigynous zone of *S. frigidum* were not observed in *S. occidentale*, though both species have a central carpellary hole and spirally inserted floral parts. The equal filaments in *S. frigidum* are considerably shorter than either of the dimorphic ones in *S. occidentale*. Raphide idioblasts were commonly seen in the upper gynoecium of *S. frigidum*, but are lacking in *S. occidentale* (Sterling, 1982; Utech, 1987). Such raphide distribution in *S. frigidum* may be a possible defense against chewing insects. Both species have bitegmic, camplyotropous ovules and flat, oblong, winged seeds.

The major differences in floral vascular patterns of *S. frigidum* and *S. occidentale* involve tepal vascularization that arises from different kinds of compound bundles and the fate of septal-ventral bundles. In the lower areas of the short flowering pedicels of *S. frigidum*, the outer tepal medians (OTM) are established first, followed by a pair of associated laterals from which the outer tepallary, staminal and dorsal bundles are derived. On the other hand, in *S. occidentale*, which has significantly longer flowering pedicels, a compound outer tepal (OT; Utech, 1987) bundle is established first, but in the same position as the OTM bundle in *S. frigidum*. The compound OT bundles in *S. occidentale* divide in the mid-pedicel to form the outer tepallary, staminal and dorsal bundles. A similar pattern is observed in the direct formation of the inner tepal medians (ITM) in *S. frigidum* versus the formation of a compound inner tepal (IT; Utech, 1987) bundle in *S. occidentale* which later divides to form an inner tepal median (ITM), tepallary laterals (ITL) and staminal (IS) bundles.

In the upper epigynous zone of *S. frigidum*, the outer lateral pairs surrounding each outer tepal median (OTM) rotate inwards and fuse along the OT radii. From this fusion plexus, a dorsal is derived first, followed by an outer stamen (OS) bundle which has reversed conducting elements. At their filament bases, the OS bundles have normally arranged conducting bundles. Except for dorsal formation, a similar set of events is associated with the formation of the inner stamen (IS) bundles, including their reversal. This pattern corresponds to that reported for the Veratreae in general (Sterling, 1982), *Amianthium muscaetoxicum* (Utech,

1986) and *Stenanthium occidentale* (Utech, 1987). The OTM and its lateral pair or the compound OT correspond to the dorsal-composite bundle reported within the Veratreae (Sterling, 1982). The ITM and its lateral pair or the compound IT, similarly, correspond to the "zwischenbündel" (Sterling, 1982).

The total outer and inner tepal vascularization in both *S. frigidum* and *S. occidentale* are derived from three bundles, a median and two tepal laterals, which were established in the upper epigynous zone. Medians do not divide or fuse, but follow a direct course to the tepal tips. The laterals, on the other hand, undergo several divisions to innervate the tepal surface. Characteristically, the tepals of *S. frigidum* have a maximum of 11 bundles; those of *S. occidentale* have seven. Though withered, the tepals are persistent in both species.

There is also a significant difference in ventral vascularization between *S. frigidum* and *S. occidentale*. In the latter, following the formation of the ventrals, a fusion septal axial (SA; Utech, 1987) with reversed conducting elements is formed and ends abruptly without fusion or further division in the lower septal arms. In *S. frigidum*, a similar bundle with reversed elements occurs, but it divides radially forming septal laterals which follow a course similar to that of the ventral with which they fuse in the upper freed gynoecium. Below this level of fusion, the ventrals supply the ovules directly, while above, the fusion products in the ventral position do. The formation of septal laterals in *S. frigidum* which later fuse with ventrals of a common origin occurs in the septal arms at the same time as the septal indentations appear.

#### CONCLUSIONS

The Mexican species *Stenanthium frigidum* has more outer and inner tepal bundles than *S. occidentale*, equal, not dimorphic filaments, septal gynoecial indentations, different patterns of ventral vascularization and raphide idioblasts in the upper carpellary zones. Both *S. frigidum* and *S. occidentale* have v-shaped tepal nectaries, while no nectaries are reported for *S. gramineum*. The chromosome number and karyotype of *S. frigidum* are unknown; neither is the relationship to *S. occidentale* with  $2n = 16$  and *S. gramineum* with  $2n = 20$ .

#### ACKNOWLEDGMENTS

The author gratefully acknowledges the loan and use of specimens from the following herbaria (CAS, CM, F, GH, LL, MO, MSC, NY, TEX, UC, UNC, US, and WIS) whose acronyms are cited in Holmgren et al., 1981. Without the kind gift of fixed floral material and use of photographic negatives by Dr. Hugh H. Iltis, long a student of the Veratreae and to whom the author is indebted, this study would have been impossible. Mr. William W. Brown deserves special thanks for his artistic aid in figure production.

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SYSTEMATICS OF AFRICAN BATS OF THE GENUS  
*EPTESICUS* (MAMMALIA: VESPERTILIONIDAE).  
2. KAROTYPES OF AFRICAN SPECIES AND THEIR  
GENERIC RELATIONSHIPS

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ABSTRACT

Bats of the genus *Eptesicus* are characterized by extreme consistency in karyotypes. All species of *Eptesicus* for which karyotypes have been reported have  $2n = 50$ ,  $FN = 48$  (Baker and Patton, 1967; Williams, 1978; Bickham, 1979a) except the African *E. capensis*, which has  $2n = 32$ ,  $FN = 50$  (Peterson and Nagorsen, 1975). We report standard karyotypes for four more species of African *Eptesicus*, none of which possess the  $2n = 50$  karyotype considered typical of the genus. *Eptesicus rendalli* ( $2n = 38$ ), *E. brunneus* ( $2n = 36$ ), *E. tenuipinnis* ( $2n = 34$ ), and *E. somalicus* ( $2n = 26$ ) all apparently have experienced numerous Robertsonian events and do not mirror the karyotypic conservatism of their New World and Palearctic relatives. These data are discussed as they apply to the currently recognized systematics of the genus *Eptesicus* and the proposed primitive karyotype of the family Vespertilionidae.

INTRODUCTION

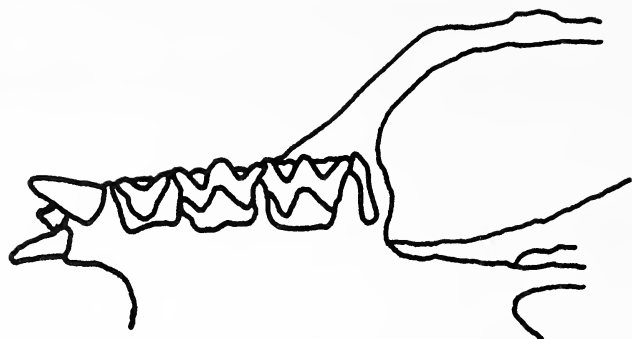
The cosmopolitan bat genus *Eptesicus* has been a source of systematic problems since its description. Various, the genus has been considered as a part of the genus *Vespertilio* along with *Pipistrellus* (Miller, 1897), and has been divided into the genera *Eptesicus* and *Rhinopterus* (Allen, 1939). Currently, there are 34 recognized species of *Eptesicus* including *Rhinopterus* (Koopman, 1984). Approximately half of these occur in Africa, where the complex interrelationships of this genus with the genus *Pipistrellus* present one of the most tangled problems of chiropteran systematics. Koopman (1975) arranged African *Eptesicus* into four groups: *E. serotinus* group including *serotinus*, *platyops*, *loveni*, *hottentotus*, and *bottae*; *E. capensis* group including *melckorum*, *brunneus*, *capensis*, *somalicus*, and *guineensis*; *E. tenuipinnis* group including *flavescens*, *rendalli*, and *tenuipinnis*; and *E. (Rhinopterus) floweri* group including *E. floweri*. He quickly commented, though, that the existing *Pipistrellus*-*Eptesicus* generic separation was almost certainly wrong. He stated that "true phyletic relationships" probably run across *Pipistrellus* and *Eptesicus* "generic lines."

The one character regularly used to distinguish the two genera is the presence (*Pipistrellus*) or absence (*Eptesicus*) of the first upper premolar (Fig. 1), which, however, repeatedly has been found to be inconsistent (Koopman, 1975; Heller

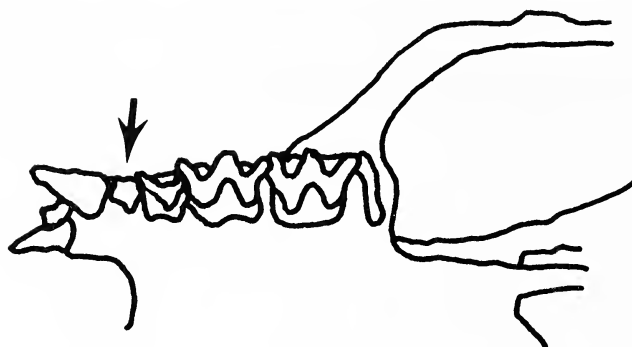
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### EPTESICUS-LIKE



### PIPISTRELLUS-LIKE

Fig. 1.—The typical character state of the first upper premolar in members of the genera *Eptesicus* and *Pipistrellus*.

and Volleth, 1984). No other character or suite of characters has yet proven capable of clearly separating the two genera (Koopman, 1975).

In several instances karyology has provided a powerful tool for clarifying systematic relationships (Baker et al., 1987). The karyotypes of thirteen species of *Eptesicus* have been reported (Table 1). With only the one exception of the African species *E. capensis*, all other species have a diploid number ( $2n$ ) of 50 and a fundamental number (FN) of 48 (Fig. 2). Heller and Volleth (1984) considered the departure of *E. capensis* from the typical *Eptesicus* karyological characteristics



Table 1.—A summary of known standard karyotypic data for the genus *Eptesicus*. SM—Submetacentric, A—Acrocentric, M—Metacentric, ST—Subtelocentric.

Species	2n	FN	X	Y	Source
<i>Eptesicus andinus</i>	50	48	SM	A	Baker and Patton, 1967
<i>Eptesicus brasiliensis</i>	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Baker et al., 1982
<i>Eptesicus brunneus</i>	36	50	SM	A	This report
<i>Eptesicus capensis</i>	32	50	SM	A	Peterson and Nagorsen, 1975
<i>Eptesicus circumdatus</i>	50	48	SM	—	Heller and Volleth, 1984
<i>Eptesicus diminutus</i>	50	48	SM	A	Williams, 1978
<i>Eptesicus furinalis</i>	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Williams, 1978
<i>Eptesicus fuscus</i>	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Bickham, 1979a
<i>Eptesicus guadeloupensis</i>	50	48	SM	A	Genoways and Baker, 1975
<i>Eptesicus hottentotus</i>	50	48	SM	—	Peterson and Nagorsen, 1975
<i>Eptesicus japonensis</i>	50	48	SM	SM	Ando et al., 1977
<i>Eptesicus lynni</i>	50	48	SM	A	Bickham, 1979a
<i>Eptesicus nilssoni</i>	50	48	—	—	Ando et al., 1977
	50	50	M	A	Zima, 1978
	50	48	M	—	Zima, 1982
<i>Eptesicus rendalli</i>	38	50	SM	—	This report
<i>Eptesicus serotinus</i>	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Vorontsov et al., 1969
	50	52	SM	SM	Fedyk and Fedyk, 1970
	50	48	SM	—	Baker et al., 1974
	50	48	SM	A	Bickham, 1979a
	50	48	SM	—	Baker and Bickham, 1980
<i>Eptesicus somalicus</i>	26	48	ST	A	This report
<i>Eptesicus tenuipinnis</i>	36	52	SM	A	This report

as sufficient reason to remove the species from the genus *Eptesicus*, and the occurrence of the typical  $2n = 50$  karyotype in *Pipistrellus circumdatus* as reason to reclassify this species as a member of *Eptesicus*. They encouraged deemphasis of the premolar as a defining characteristic and suggested that the conservative karyological traits of *Eptesicus* were more reliable in differentiating between the two genera. Hill and Francis (1984) questioned the karyologically based arrangement of Heller and Volleth (1984), however, because chromosomal data were not yet available for many species of these nominal genera. We examined standard karyotypes prepared from bone marrow (Fig. 3–5) of four additional species of *Eptesicus* from Somalia and Cameroon (Fig. 6) and found none to fit the presumed chromosomal characteristics of the genus.

#### METHODS

Karyotypes were obtained from 34 specimens of the genus *Eptesicus* using humeral bone marrow preparations made in the field by the *in vivo* incubation method as described by Robbins and Baker (1978). Nomenclature of chromosome morphology is that of Patton (1967). The presence or absence of the first upper premolar was determined for 19 of the karyotyped specimens and 22 other specimens of the same species. All specimens examined are housed in The Carnegie Museum of Natural History (CM). Slides are housed at The Carnegie Museum of Natural History (SP) or Texas A&M University (TK).

#### SPECIMENS EXAMINED

*Eptesicus brunneus*. Cameroon: 16 km S, 2 km E Yaounde, 1 F; 9 km S, 10 km W Yaounde, 4 F; 7 km S, 8 km W Yaounde, 2 F; 20 km S, 9 km E Ambam, 1 F, 1 M.



Fig. 2.—Standard karyotype of *Eptesicus lynni* (TK 8312),  $2n = 50$ ,  $FN = 48$ .

*Eptesicus rendalli*. Somalia: S.N.A.I. Sugar Plantation,  $1\frac{1}{2}$  km S,  $\frac{1}{2}$  km E Giohar, 4 F, 1 M.

*Eptesicus somalicus*. Somalia: S.N.A.I. Sugar Plantation,  $1\frac{1}{2}$  km S,  $\frac{1}{2}$  km E Giohar, 8 F, 5 M.

*Eptesicus tenuipinnis*. Cameroon: 23 km S, 1 km E Yaounde, 1 F, 1 M; 9 km S, 10 km W Yaounde, 2 F, 2 M; 20 km E Ambam, 1 F.

### RESULTS

Only two individuals, members of *E. tenuipinnis*, showed the presence of the first upper premolar. In one it was present only on the left side of the jaw. In the other it was present only on the right side of the jaw.

The standard karyotype of *E. tenuipinnis* is  $2n = 36$ ,  $FN = 52$  (Fig. 3A). There is a graded series of seven pairs of large to medium-sized metacentric and submetacentric autosomes and two pairs of small submetacentric to subtelocentric chromosomes (Fig. 3A, open arrows). The remaining eight pairs of autosomes are acrocentric. The X is a medium-sized submetacentric chromosome and the Y is a small acrocentric chromosome.

The standard karyotype of *E. brunneus* is  $2n = 36$ ,  $FN = 50$  (Fig. 3B). This karyotype consists of seven pairs of large to medium-sized metacentric and submetacentric chromosomes but has only one small pair of subtelocentric chromosomes (Fig. 3B, open arrow). There are nine pairs of acrocentric autosomes, one of which bears a secondary constriction near the centromere (Fig. 3B, solid arrow). The X is a medium-sized submetacentric chromosome and the Y is a small acrocentric chromosome. The additional pair of sex chromosomes in this figure is from SP 0318.

The standard karyotype of *E. rendalli* is  $2n = 38$ ,  $FN = 50$  (Fig. 4). The

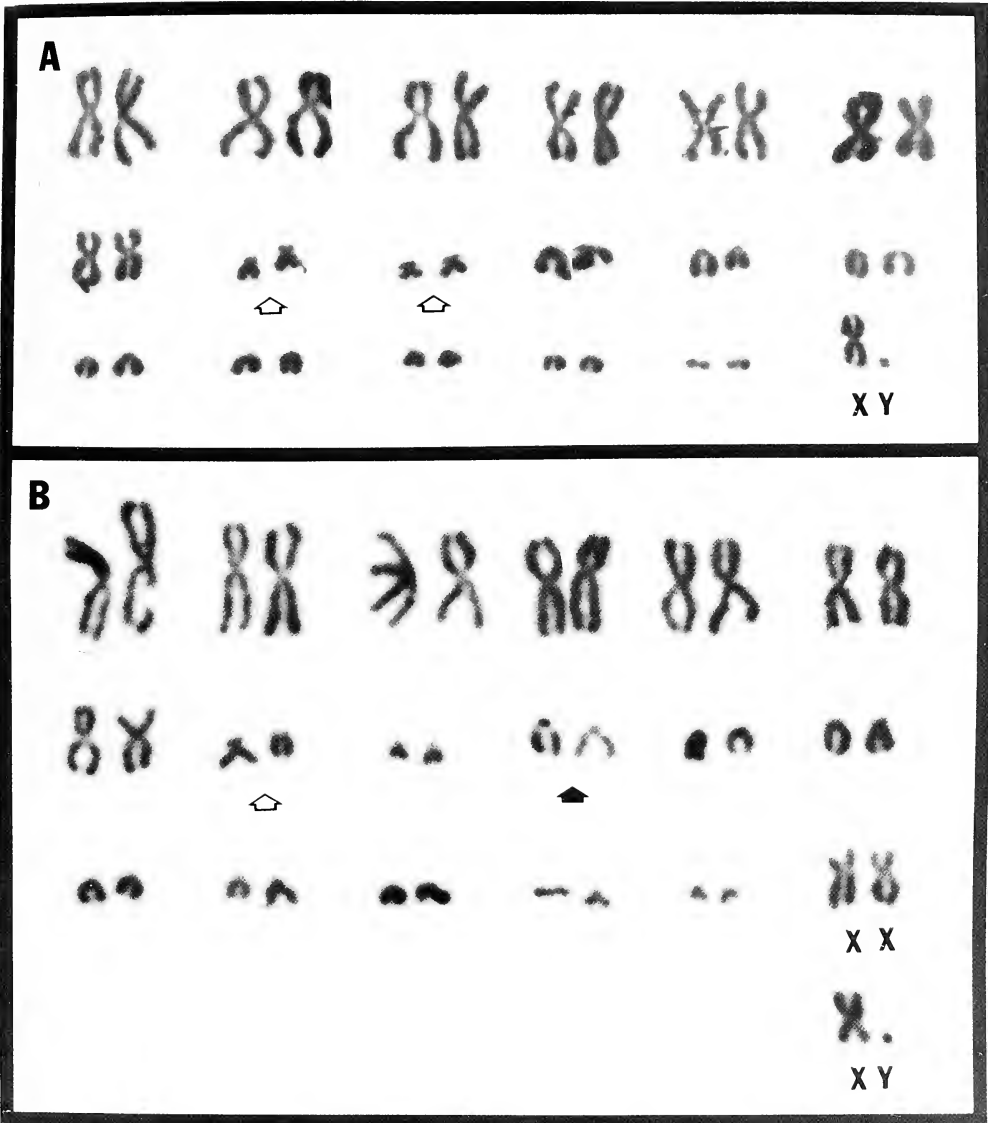


Fig. 3.—A. Standard karyotype of *Eptesicus tenuipinnis* (CM 58531),  $2n = 36$ ,  $FN = 52$ . B. Standard karyotype of *Eptesicus brunneus* (CM 58510),  $2n = 36$ ,  $FN = 50$ .

autosomal complement includes five pairs of large metacentric to submetacentric chromosomes, one pair of medium-sized metacentric chromosomes, and one pair of small subtelocentric chromosomes (Fig. 4, open arrow). The remaining 11 pairs of autosomes are acrocentric, grading in size from medium to very small. A secondary constriction is prominently apparent near the centromere of one of the larger pairs of acrocentric chromosomes (Fig. 4, solid arrow). The X is a submetacentric chromosome.

The standard karyotype of *E. somalicus* is  $2n = 26$ ,  $FN = 48$  (Fig. 5). The



Fig. 4.—Standard karyotype of *Eptesicus rendalli* (CM 85307),  $2n = 38$ ,  $FN = 50$ .

autosomal complement is composed entirely of 12 pairs of metacentric to submetacentric chromosomes grading from large to small. The secondary constriction apparent on acrocentric chromosomes in other species is found near the centromere of a medium-sized pair of submetacentric chromosomes in this species (Fig. 5, solid arrow). The X is a medium-sized submetacentric chromosome and the Y is a small acrocentric chromosome.

The standard karyotype of *E. lynni* is  $2n = 50$ ,  $FN = 48$  (Fig. 2). Autosomes consist of a graded series of 24 pairs of acrocentric chromosomes. A prominent secondary constriction is apparent near the centromere of one medium-sized pair (Fig. 2, solid arrow). The X chromosome is submetacentric and the Y chromosome is minute and acrocentric. This karyotype is exemplary of chromosomal complements of 12 other species of this genus from throughout its range (Table 1).

#### DISCUSSION

If karyological characteristics can be considered valid criteria for delineation of systematic relationships (Baker, 1984; White, 1978), then serious consideration must be given to redrawing the systematic lines defining the genera *Pipistrellus* and *Eptesicus*. At least two interpretations are available for the karyotypic trends observed in African *Eptesicus*. Of all the mammals karyologically studied, *Eptesicus* has been considered among the most conservative (Baker and Bickham, 1980; Bickham, 1979a). Species from North and South America, Europe, Africa, and Asia all have an essentially identical karyotype. Prior to this study, the only species which did not possess the typical karyotype was the African *E. capensis*.

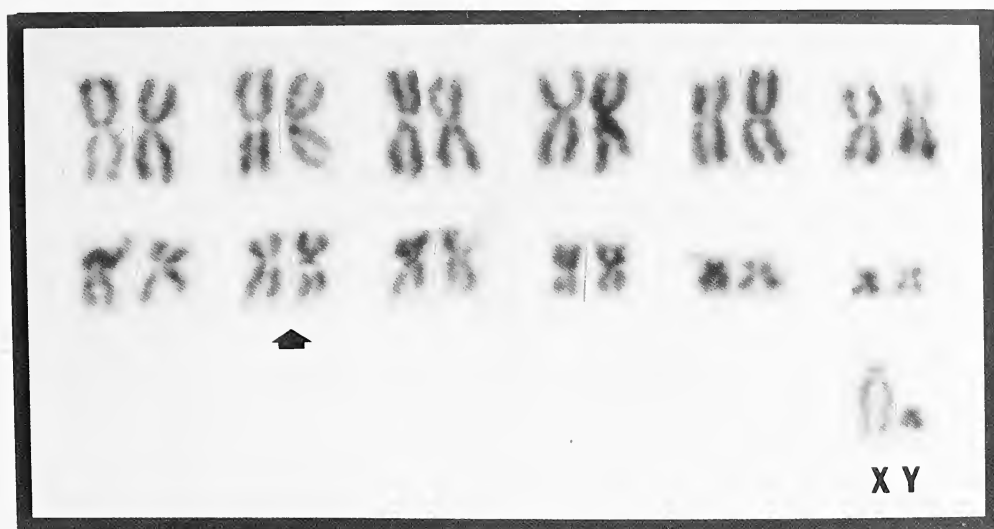


Fig. 5.—Standard karyotype of *Eptesicus somalicus* (CM 85320),  $2n = 26$ ,  $FN = 48$ .

We add four more species of African *Eptesicus* which do not follow the conservative chromosomal pattern considered typical for the genus.

The genus *Eptesicus* might be much more karyotypically variable than initially thought, with the center of variability located in Africa. If this is the case, species such as *E. capensis*, which Heller and Volleth (1984) would remove from the genus on a karyotypic basis, would have to be reevaluated. Also, if *Eptesicus* is, indeed, among the karyotypically more variable genera of Vespertilionidae, additional questions are raised regarding patterns of chromosomal evolution within the family. The typical *Eptesicus* karyotype has been postulated as being like the ancestral karyotype for the family (Stock, 1983). This karyotype is found in no other genus of the family except *Histiotus*. The other proposed ancestral karyotype of  $2n = 44$ ,  $FN = 50$ , occurring in the genus *Myotis* (Bickham, 1979b), is found in several other genera of the subfamily Vespertilioninae and in two of the remaining four subfamilies (McBee et al., 1986). Bickham (1979a) proposed a derivation of the *Eptesicus* karyotype from the *Myotis*-like ancestral karyotype through a process of six centric fissions. Assuming that the *Myotis*-like karyotype is primitive for the family and that these chromosomally more variable forms are indeed *Eptesicus*, chromosomal evolution within the genus may have proceeded first by a series of centric fissions and then by a series of centric fusions independent of other vespertilionine lines of chromosomal evolution. G-banding analysis of these taxa will allow identification of patterns of fusion among the different chromosome arms and may elucidate the track of chromosomal evolution within the family.

Alternatively, if the genus *Eptesicus* can be defined by the possession of  $2n = 50$  and  $FN = 48$ , at least five species currently recognized as members of the genus must be reclassified. The genus *Pipistrellus* is characterized by broad chromosomal variability (Bickham, 1979a; McBee et al., 1986) rather than one distinct karyotypic pattern. All five atypical *Eptesicus* karyotypes fit within the spectrum of known *Pipistrellus* karyotypes. It is tempting to allocate these five species to

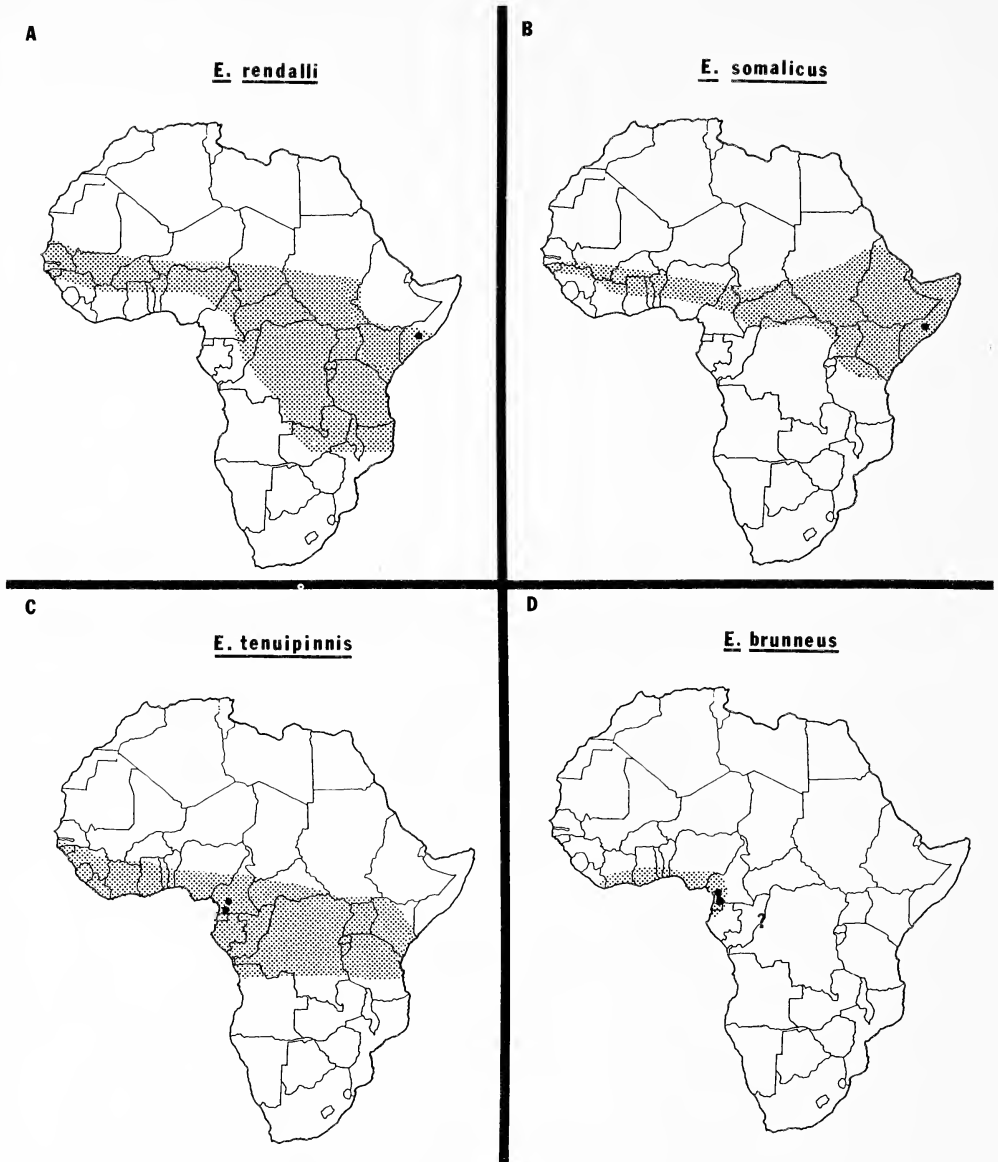


Fig. 6.—Range maps of four species of African *Eptesicus*. Shaded areas represent currently recognized ranges. Black dots represent collecting localities of individuals examined in this study.

the genus *Pipistrellus*, but such a move without more extensive analysis of both standard and G-banded karyotypes and morphology would be premature. At this point, neither interpretation of these karyotypic data is more robust than the other. Both stress the great need for extensive redefinition and revision of the genus *Eptesicus*, however, and emphasize that no single trait, whether morphological or karyological, is powerful enough to untangle the systematic lines between *Pipistrellus* and *Eptesicus*.

Of the species in sub-Saharan Africa presently allocated to *Eptesicus*, *E. hot-*

*tentotus* from southern and eastern Africa (Schlitter and Aggundey, 1986) and *E. platyops* from western Africa (Ib'añez and Valverde, 1985) are typical *Eptesicus* and related to *E. serotinus* and *E. fuscus*. Only *E. hottentotus* has been karyotyped (McBee et al., 1986) and it agrees with the typical *Eptesicus* pattern. The remaining species fall into two groups. One species in Sudan, *E. floweri*, is placed in the subgenus *Rhinopterus* (Koopman, 1975) but a karyotype has not been reported for this species. For the remaining species with karyotypes showing an affinity with *Pipistrellus*, the subgenus *Neoromicia* proposed by Roberts (1926) for the species *Eptesicus zuluensis* is available.

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REVISION OF THE WIND RIVER FAUNAS, EARLY  
EOCENE OF CENTRAL WYOMING. PART 8. FIRST FOSSIL  
LIZARD EGG (?GEKKONIDAE) AND LIST OF  
ASSOCIATED LIZARDS

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ABSTRACT

A small fossil egg from the Lostcabinian (early Eocene, CM loc. 1040) of the Wind River Formation, Wyoming, is the first unequivocal record of a fossil lizard egg. It has a shell structure similar to that of rigid-shelled eggs of modern geckos, especially *Tarentola delalandii*. The unique eggshell structure of Recent geckos warrants recognition of a fourth type of rigid eggshell in addition to those of chelonians, crocodilians and birds. At least 22 species of lizards are represented by skeletal material at the fossil egg locality, including anguids, necrosaurids, agamids, varanids, xantusiids, xenosaurids, iguanids, and teiids.

INTRODUCTION

In 1984, paleontologists from The Carnegie Museum of Natural History collected several fossil eggs from early Eocene (late Wasatchian, Lostcabinian) horizons of the Wind River Formation in central Wyoming. One of these eggs is small (8-9 mm diameter), has a rigid eggshell, and represents the first unequivocal record of a fossil lizard egg. It resembles eggs of living geckos, the only extant lizards with rigid eggshells. Other fossil squamate eggs have been mentioned in the literature (Meyer, 1867) and identified in some collections on the basis of gross features of the specimens, which may not be diagnostic.

The eggshell structure of only a few species of squamates has been studied in detail; that of geckos has been mentioned only briefly (Schmidt, 1957; Hirsch, 1983, 1985; Packard et al., 1982). However, studies of the shell microstructure (Erben and Newesely, 1972), and the biominerals of the shell membrane and calcitic layer (Krampitz et al., 1972, 1974) established that gecko eggshells differ from those of birds, crocodilians and chelonians, and represent a fourth type of rigid eggshell.

Fossil geckos are first known from the late Paleocene of Brazil and the late Eocene of Europe (Estes, 1983). In North America, the earliest geckos are known from the early Miocene of Florida, but have been identified with question from the late Middle Eocene of the Mission Valley Formation, California.

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Table 1.—*Fossil lizards known from skeletal material from the B-2 horizon at Buck Spring (CM loc. 1040), Lost Cabin Member, Wind River Formation.*

Taxon	No. specimens
Anguidae	
Diploglossinae sp.	18
<i>Xestops</i>	14
? <i>Ophisaurus</i> sp.	3
<i>Machaerosaurus</i> sp.	2
<i>Glyptosaurus donohoei</i>	1
cf. <i>Gerrhonotus</i> sp.	1
Anguinae sp.	1
Xantusiidae	
Xantusiidae sp. A	9
Xantusiidae sp. B	3
Xantusiidae sp. C	3
Xenosauridae	
<i>Exostinus</i> sp.	6
Agamidae	
<i>Tinosaurus</i> n. sp.	4
Iguanidae	
Iguanidae sp. A	7
Iguanidae sp. B	4
Iguanidae sp. C	3
<i>Parasauromalus</i> sp.	1
Varanidae	
Varanidae sp.	3
Necrosauridae	
<i>Necrosaurus</i> sp.	2
Teidae	
?Teidae sp.	1
Sauria	
<i>Oligodontosaurus</i> sp.	2
"Scincomorpha" sp.	3
Sauria n. gen.	2
Sauria undetermined	100+

## LOCALITY AND ASSOCIATED FAUNA

The fossil egg was recovered from the Buck Spring Quarries (Quarry 1, Horizon B-2, CM loc. 1040) in the type area of the Lost Cabin Member of the Wind River Formation. As described elsewhere (Stucky and Krishtalka, 1987; in press), the geology of the locality and mode of preservation of the fossil vertebrates are unique among known Wind River Formation localities. The eggshell-bearing horizon consists of alternating thinly-laminated mudstone and limestone couplets, which were apparently deposited in freshwater ponds and/or well-drained swamps within 250 m of the nearest permanent stream.

At least 22 species of lizards are known from dental and skeletal remains from the B-2 horizon (Table 1). This is the highest diversity recorded among known Eocene lizard faunas. However, no gekkonid skeletal material has been positively identified from this horizon. One of the lizards, *Glyptosaurus*, is here considered a senior synonym of *Eoglyptosaurus*. Study of the type species of the latter, *E.*

Table 2.—Size, shell thickness and status of modern gecko and fossil egg.

Specimens	Egg size (mm)	Shell thickness (mm)	Status of egg
Eocene egg			
CM 46668/HEC 321	8 × 9	0.04–0.05	—
<i>Tarentola delalandii</i>			
UCM OS1142/HEC 357	9 × 10	0.06–0.07	hatched
<i>T. mauritanica</i>			
UCM OS1129/HEC 408	11 × 12	0.09–0.1	?infertile
<i>Phelsuma madagascariensis</i>			
UCM OS1130/HEC 125	13 × 15	0.14–0.16	hatched
<i>Gekko gekko</i>			
UCM OS1143-1/HEC 391-1	21 × 19	0.27–0.34	?infertile
<i>G. gekko</i>			
UCM OS1143-2/HEC 391-2	21 × 19	0.27–0.34	?infertile
<i>G. gekko</i>			
UCM OS1143-3/HEC 391-2	21 × 19	0.27–0.34	embryo/early stage
<i>Lepidodactylus lugubris</i>			
Erben and Newesely, 1972	—	?0.9	—
<i>Hemidactylus turcicus</i>			
Packard et al., 1982	—	?0.06	—

*donohoei* (including the holotype, USNM 18316), reveals that it has a linear band of pterygoid teeth, a feature also found in *G. sylvestris*, the type species of *Glyptosaurus* (Sullivan, 1986). Sullivan erred in separating *Eoglyptosaurus* from *Glyptosaurus* on this characteristic, as well as on the presence of raised subconical osteoderms, which appears to vary allometrically in *G. donohoei* (Stucky, unpublished data).

In addition to the lizard eggshell and skeletal material, relatively complete and well preserved specimens of fossil mammals, turtles, birds, snakes, amphibians, crocodilians and fish have been recovered from the Buck Spring Quarries. The B-2 horizon also preserves fossil roots and stems of plants (carbonate-replaced and lignified), avian eggshells, algal skeletal grains, and rarely, gastropods and decapod exoskeletons.

#### MATERIAL AND TECHNIQUES

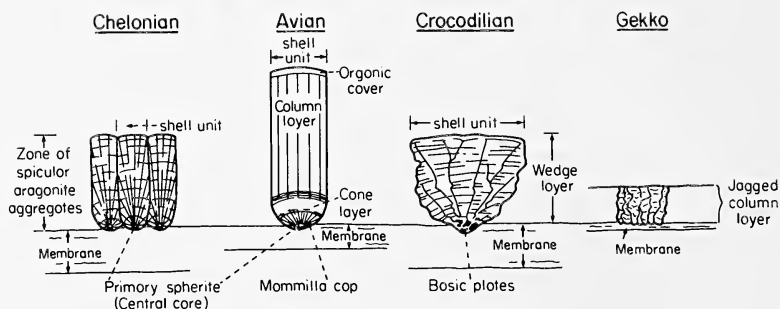
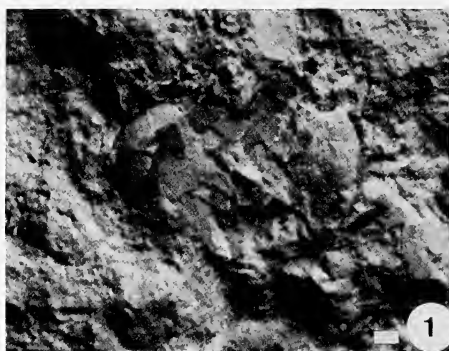
Specimens of modern and fossil eggshell (Table 2) were studied using polarizing light microscopy (PLM), scanning electron microscopy (SEM) and X-ray diffraction (XRD). Methods described in Hirsch (1979, 1983) and Packard et al. (1984) were followed as far as the very delicate and fragile nature of the specimen allowed. Three small shell fragments were detached from the fossil egg, the remainder of which is still preserved in the surrounding block of matrix (CM 46668, Fig. 1). These fragments were too fragile to be treated with chemicals or cleaned in an ultrasonic bath. Thus the outer and the inner surfaces are somewhat contaminated by secondary deposits or preservatives. However, fresh fractures of the shell permitted examination of radial (edge) sections. Tangential sections of the fossil specimen could not be prepared. The status of the egg (fertilized or unfertilized, stage of incubation) was known in three cases for the modern eggshells.

Abbreviations: CM, The Carnegie Museum of Natural History; HEC, Hirsch Egg Collection; UCM, University of Colorado Museum; USNM, U.S. National Museum.

#### RESULTS

##### *Modern Rigid-Shelled Gecko Eggs*

The rigid eggshell, one of the three main kinds of amniote eggshells (Hirsch, 1983, 1985; Packard and Packard, 1980), is the most likely to become fossilized. The calcareous layer of these eggshells is very thick in comparison to the underlying membrane and is composed of well-defined, interlocking, more or less spherulitic



2

Fig. 1, 2.—1. Fossil egg embedded in matrix. Scale = 1 mm. 2. Terminology and structure of the four types of modern rigid eggshells.

shell units that are nucleated on the membrane. Among amniotes with rigid-shelled eggs, a typical shell structure has been recognized for birds, crocodilians and turtles (Schmidt, 1943, 1957; Schmidt and Schoenwetter, 1943; Erben and Newesely, 1972; Hirsch, 1983, 1985). The characteristic structure of rigid-shelled gecko eggs differs from these types and warrants classification as a fourth type (Fig. 2; see also Erben and Newesely, 1972; Krampitz, 1972).

Gecko eggshells are composed of a thin inner membrane overlain by a comparatively thick calcareous layer (0.06–0.34 mm, see Table 2), which is covered by a more or less fibrous, organic cuticle. The surface of the cuticle can be an open network of fibers, or relatively smooth, or bumpy as a result of the nodes of the underlying calcareous layer.

The calcareous layer, as in the avian eggshell, is made up of tightly abutted calcite columns extending from the membrane to the outside of the shell. In edge view, the columns interlock along uneven, jagged surfaces (Fig. 4, 5) and thereby differ from the spherulitic, even, interlocking crystal pattern found in avian eggshells. The jagged columnar structure is typical for the first four species examined in Table 2 and has also been observed in *Lepidodactylus* and *Hemidactylus* (Erben and Newesely, 1972; Packard et al., 1982). In radial view the columns show horizontal and sometimes almost lamellar layering. Under PLM, faint columnar extinction patterns can be observed. In tangential thin sections, the pattern of the columns is polygonal, but randomly interlocking. As in all other shell types, the gecko eggshell varies from one point to another in columnar size and shell thickness.

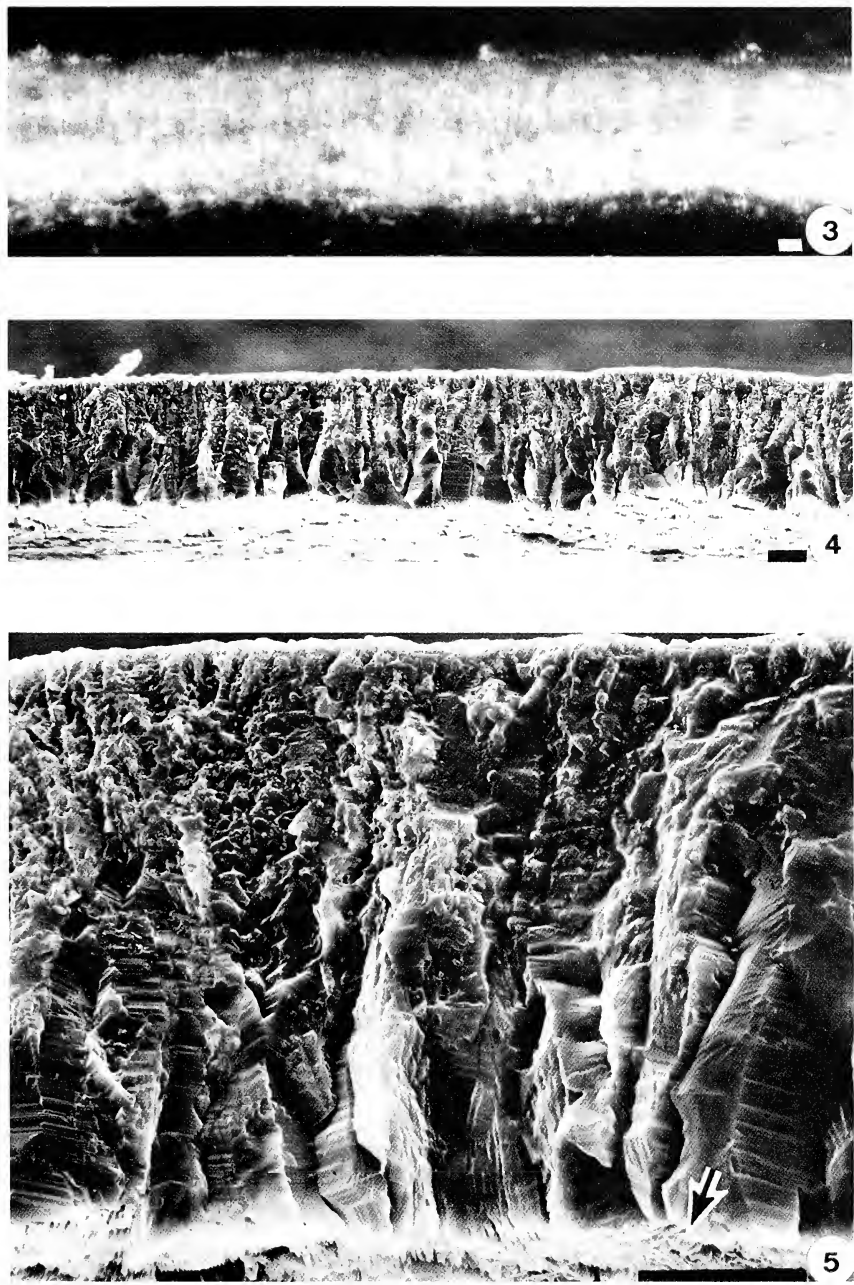


Fig. 3-5.—*Tarentola delalandii* eggshell (scale = 10  $\mu$ ). Outside of shell is up. 3. Radial thin section viewed under polarized light. Note that columnar structures are somewhat narrower than in the fossil egg (see Fig. 6). 4. Photomicrograph of radial view (edge) of eggshell. 5. Enlargement of Fig. 4. Note the minute crystals on mammillary column faces (arrow).

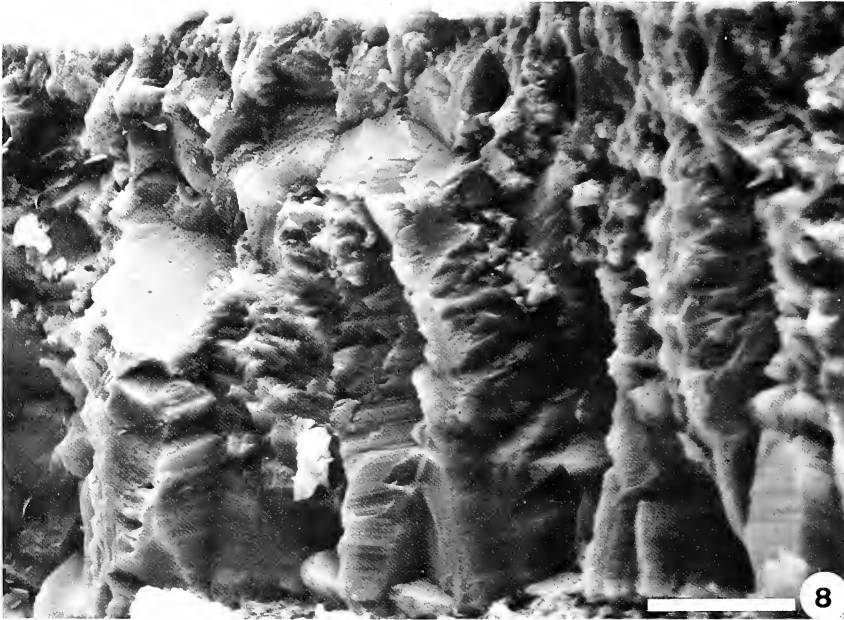
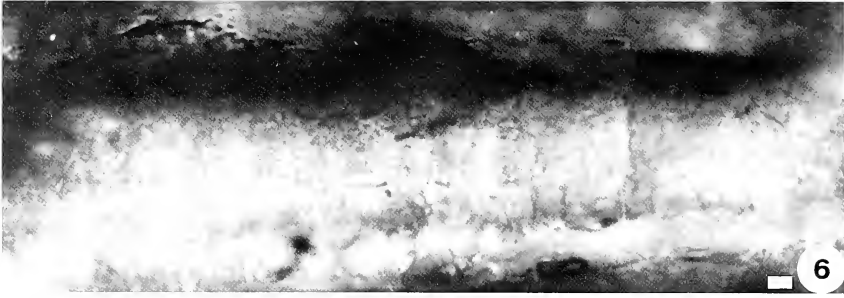


Fig. 6-8.—Fossil eggshell (scale = 10  $\mu$ ). Outside of shell is up. 6. Radial thin section viewed under polarized light. Note faint columnar structures. 7. Micrograph of radial view (edge) of eggshell. Note similarity to radial view in Fig. 4. 8. Enlargement of Fig. 7. Note jagged columnar structure and horizontal layering.

A shell unit structure (see Fig. 2) has not yet been observed in gecko eggshells, either with SEM or PLM. It also has not been established how the calcite columns are nucleated or how they are fastened to the membrane. Central cores, such as occur in avian and chelonian eggshells, and basal plate groups, as in crocodilian eggshells, have not been observed. In unfertilized and fertilized but unhatched eggs the basal tips of the columns are tightly fastened to the membrane; in hatched eggs this membrane is much less securely fastened.

The shape of the basal tip or face of the columns in gecko eggs varies inter-specifically. Variation within a species, observed in several eggs with different incubational histories, may be partly a result of dissolution of columns caused by the withdrawal of calcium from the eggshell by the developing embryo (Packard et al., 1984). In hatched eggs, the basal faces are studded with minute crystals pointing toward the inside of the egg. In eggs of unknown hatching status, round or lumpy tips can be observed.

### *The Wind River Fossil Egg*

The Eocene egg (CM 46668) was compressed during fossilization, but its original shape was apparently spheroidal and measured approximately 8–9 mm in diameter. Eggshell thickness is 0.04–0.05 mm. Like the eggshell of living gekkonids, the fossil eggshell is rigid and does not have the unit structures typical of chelonian, crocodilian or avian eggshells (Fig. 2).

In size and shell structure, the fossil egg is most similar to that of *Tarentola delalandii* (Fig. 4, 5, 7, 8). In both, the columns are wide and strongly jagged, and the horizontal layering (growth lines) is very distinct (Fig. 5, 8). These features are not as pronounced in other living species of geckos that have been studied. Both specimens also exhibit a faint columnar extinction pattern when rotated under crossed nicols (Fig. 3, 6).

The outer surface of the fossil egg is relatively smooth, with no indication of nodes or other sculpturing. Under high magnification, some crystal structure of the column heads is visible.

It is not clear whether the details of the inner surface of the fossil shell reflects original morphology or diagenetic alteration. Low magnification (SEM) reveals a very faint indication of a polygonal pattern, which may represent the faces of dissolved column tips as described above for some hatched gecko eggs. However, unlike *Tarentola* (Fig. 5), high magnification does not reveal distinct small crystals, only small crystalline nodes, perhaps a result of diagenetic recrystallization.

Microprobe and X-ray fluorescence studies determined that the fossil eggshell is composed of calcium carbonate. X-ray diffraction analysis could not distinguish between aragonite and calcite because of the limited amount of fossil material; however, the crystalline structure strongly suggests calcite.

### CONCLUSIONS

A preliminary study of modern rigid-shelled gecko eggs indicates that the jagged, columnar structure of the calcareous layer distinguishes them from recognized types of avian, crocodilian and chelonian eggshells. Based on this diagnostic feature, recognition of a fourth type of rigid eggshell is warranted, although interspecific variation in the microstructure of the jagged columns and cuticle occurs among geckos.

The Early Eocene egg from the Wind River Formation is the first such record for fossil lizards. Two of its features—the rigid shell and jagged, columnar structure

of the calcareous layer—are diagnostic. They are known only among extant geckos, and closely resemble the condition in *Tarentola*.

Fossil gecko bones are unknown in the Wind River Formation, although some of the lizard material is provisionally identified and may represent gekkonids. Nevertheless, the fossil egg may have belonged to one of the other lizards recovered from the B-2 horizon in the Wind River Formation at Buck Spring.

#### ACKNOWLEDGMENTS

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TAXONOMIC NOTES ON SOME AFRICAN WARBLERS  
(AVES: SYLVIINAE)

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## ABSTRACT

Notes on geographic variation are presented for six species of African warblers: *Chloropeta similis*, *Cisticola chiniana*, *Apalis jacksoni*, *Apalis porphyrolaema*, *Apalis cinerea*, and *Sylvietta leucophrys*. Two new subspecies of *C. chiniana* are described from Tanzania, and one new subspecies of *S. leucophrys* from Uganda.

## INTRODUCTION

During the course of incorporating the Twomey collections of African birds (see Parkes, 1980 for history of these collections) into the main series at The Carnegie Museum of Natural History, I encountered several taxonomic problems that could not be solved with the material at hand. The pertinent specimens were therefore taken to the American Museum of Natural History for further study. As a followup, critical specimens of certain species were borrowed from other museums (see Acknowledgments). This paper presents the results of these studies. Species discussions are given in the sequence of Traylor (1986). The present paper was essentially completed before the publication of that book, but minor modifications have been made in the manuscript to cite Traylor where appropriate. Distances are given metrically *except* when cited from original labels or publications.

Abbreviations for museums: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; BM(NH), British Museum (Natural History); CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; LACo, Los Angeles County Museum; MCZ, Museum of Comparative Zoology, Harvard University; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum of Natural History; YPM, Peabody Museum of Natural History, Yale University.

*Chloropeta similis*

Direct comparison of a series of 9 topotypes of *similis* from Mt. Kilimanjaro with 11 topotypes of *kenya* Sharpe from Mt. Kenya indicates that Friedmann (1937:234) was correct in synonymizing the latter with *similis*. Sharpe (1901), in describing *kenya*, compared it only with *natalensis*, now considered a separate species, and apparently overlooked the description of *similis* by Richmond in 1897. In series, the Mt. Kilimanjaro birds average faintly browner, less greenish on the dorsum, but the series overlap broadly. There appears to be no significant change in dorsal coloration owing to museum age ("foxing"); all of the Mt. Kilimanjaro series were collected in 1920-1921, but Mt. Kenya specimens were taken in 1926, 1936, and 1963, and show no age-related differences.

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Friedmann (1937:234) did not examine specimens of *Chloropeta schubotzi* Reichenow, described from the Rugege Forest, east of Lake Kivu (now in Rwanda), but synonymized it with *similis* on the basis of notes by other authors. Reichenow (1908) compared his *schubotzi* only with "*Ch. major*" (= *Chloropeta natalensis major* of Angola) and not with either *similis* or *kenya*.

Comparison of one topotype and a series of 19 specimens from Kivu, Baraka, and Ruwenzori assigned to "*schubotzi*" at the AMNH with the 20 specimens of *similis* from Kenya mentioned above failed to demonstrate the darker back attributed by some authors to this supposed western race. I concur with Friedmann and others who have synonymized *schubotzi* with *similis*.

Within Kenya, comparisons were made between the Mts. Kilimanjaro/Kenya series and a series from the Aberdare Range and the vicinity of the Mau Escarpment, just to the west. The Aberdare/Mau series, which triggered this investigation, averages noticeably brighter (yellowier) above, especially on the forehead, but the differences are subtle and individual specimens would be difficult to allot. The best course seems to be to continue to consider this species to be monotypic, as Traylor (1986) has done, admitting that there are some incipient tendencies toward geographic differentiation.

### *Cisticola chiniana*

Before beginning the discussion of this species, a note on the plumages of *Cisticola* is in order. It is well known that some populations of this genus have two distinctive seasonal plumages, whereas others have the same aspect all year round. It is fairly clear from the account by Lynes in his classical monograph of this genus (1930:41) that those forms that do not change in appearance *do not* nevertheless have two molts annually: "... a perennial dress which is renewed only once a year during a brief off-season." As the term "off-season" is sometimes used in older literature in connection with a "non-breeding" or "eclipse" plumage, it should be made clear that Lynes used it merely to indicate a *time of year* when no breeding takes place, i.e., during the molt. Lynes used the terms "perennial mode" and "seasonal mode" to differentiate the one-plumage and two-plumage annual cycles in *Cisticola*. His description of the plumage sequence in the perennial mode (p. 44) makes it clear that his "immature dress" is the First Basic Plumage of Humphrey and Parkes (1959), which is highly variable, among species and undoubtedly among populations of *Cisticola*, as to duration and appearance. Even though the terms may seem inappropriate for Africa, Lynes uses "winter dress" and "summer dress" for the seasonal plumages of *Cisticola*; these correspond functionally to the non-nuptial and nuptial plumages of many authors, and from a homology viewpoint, to the Basic and Alternate plumages of Humphrey and Parkes (1959). The Alternate Plumage has thus evolved in some but not all populations of *Cisticola*; it is particularly interesting to note that the Basic Plumage of some of the forms with the perennial mode resembles in color the Alternate Plumage and in others the Basic Plumage of those forms with a two-plumage cycle. One of the few species in which both modes can be found, with implications for geographic variation, is *Cisticola chiniana*.

Geographic variation in this species in Tanzania is complex. Lynes (1930) attributes four races to this country: *procera* Peters in the southeast, *heterophrys* Oberholser in the east, *fischeri* Reichenow in the central and northern interior, and *victoria* Lynes in the Victoria Nyanza basin in the north. Vincent (1944) divided the range attributed to *procera* by Lynes into northern and southern

components, describing the more northern subspecies (the one that would reach southeastern Tanzania) as *emendata*, and stating that this action had the support of Lynes, who had been dissatisfied with his own 1930 concept of *procera*. White (1962) substantially altered the arrangement of Tanzanian races of *C. chiniana*. He synonymized *emendata* with *procera*, thus returning to the treatment of Lynes for the southeastern area. He synonymized *victoria* with *fischeri*, thus admitting only one subspecies across northern and north-central Tanzania, from the eastern and western shores of Lake Victoria south to Tabora. However, he added another subspecies to the Tanzanian list. He identified the populations of the northeastern highlands, along the Kenya border, as *ukamba* Lynes, described from the eastern plateau region of Kenya, and those of Lake Rukwa, in the southwest, as *fortis* Lynes, described from interior Angola. Britton (1980) essentially followed White's treatment of subspecific ranges, although without mentioning Tanzania in the range of *ukamba*.

Lynes characterized his race *victoria*, with a type locality on the east side of Lake Victoria, as larger and more boldly marked than *fischeri*, with "the markings giv[ing] the upper side as much a striped as mottled appearance." In synonymizing *victoria* with *fischeri*, White (1962) attributed the large size of the specimens from along the south and east sides of Lake Victoria to intergradation with *humilis* Maderasz of the West Kenya highlands. He did not address the subject of color. I have compared 5 near-topotypical males of *victoria* with five males of typical *fischeri*. The two series differ in size as stated by both Lynes and White; in addition, the black streaks of the mantle are distinctly broader in *victoria*, and the crown is darker brown, with more conspicuous black centers to the feathers; in *fischeri* the crown feathers are only slightly darker in the center than on the edges. The difference in appearance of the crown is well expressed by Lynes's comparison between "striped" (*victoria*) and "mottled" (*fischeri*). There is no difference in underparts color. A series from the Serronea River, in the Serengeti region (ANSP) is more or less intermediate between *victoria* and *fischeri*, and a rather worn male from 10 miles S of Mwanza, on the south shore of Lake Victoria (BM[NH]), also appears intermediate. I am skeptical about White's identification of *victoria* as a population of *fischeri* whose large size is attributable to intergradation with *humilis*. The latter is conspicuously paler dorsally than *fischeri* with more contrasting edges to the tertials, and there is no sign of approach to the color of *humilis* among specimens of *victoria*. Furthermore, the dorsal streaks of *humilis*, although more conspicuous than those of *fischeri*, are as narrow as those of that race, so that the broader streaks of *victoria* cannot be attributed to intergradation with *humilis*. It would appear that *victoria* Lynes is worthy of acceptance, but its exact range and relationships with bordering races will require examination of better material than is now available. I have not seen specimens that would permit me to evaluate the validity of *emendata* Vincent, so I follow White in using the name *procera* for the southeastern Tanzanian populations, without prejudice. I do agree with White that the populations of the Kilimanjaro region, northwest to Lake Natron, are indistinguishable from *ukamba*. Specimens from Loliondo, northwest of Lake Natron, however, are nearest the other Kenyan race, *humilis*. These two races differ more in size than in color; I am unable to appreciate most of the differences suggested by figs. 38 and 39, plate 10, of Lynes (1930), except the more buffy, less grayish edgings of the tertials of *humilis*; the ground color of the crown averages duller in *humilis*, and, contrary to the figures cited above, the streaks on the crown are more distinct in *humilis* than in *ukamba*.

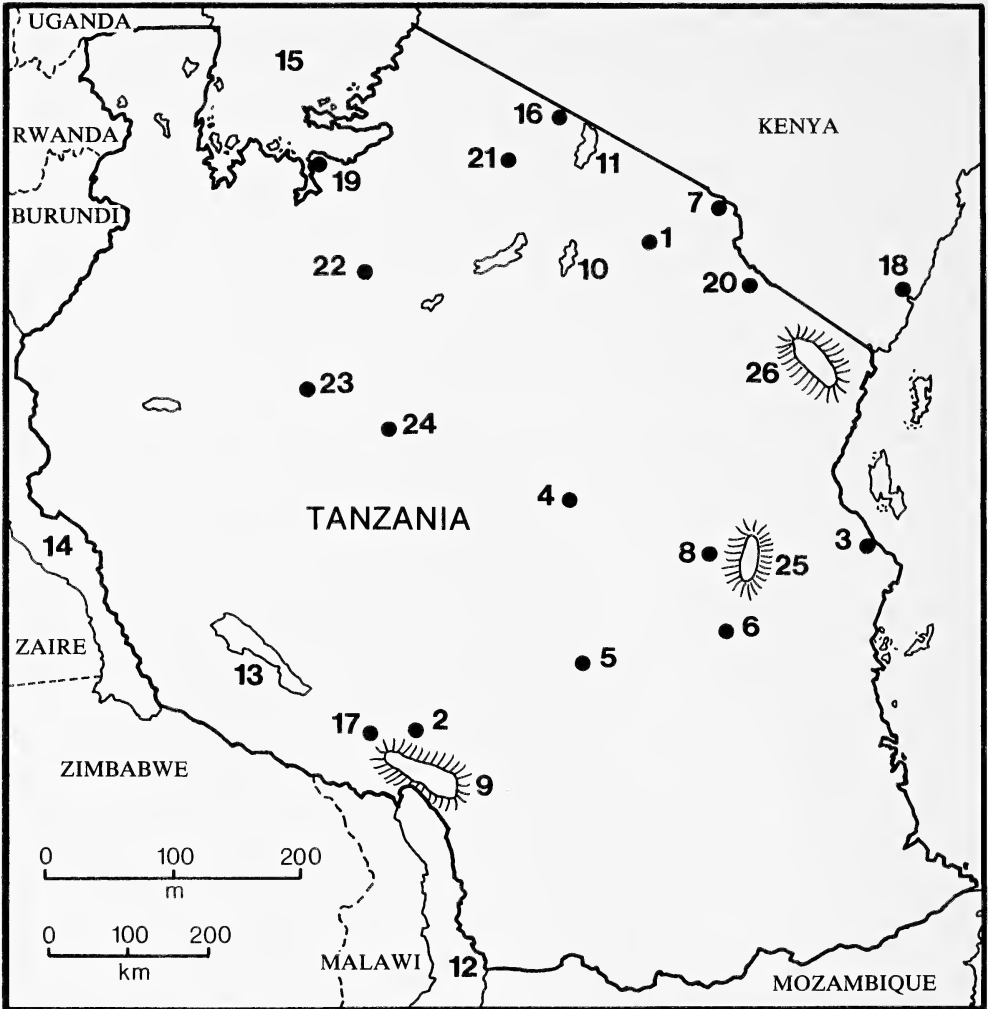


Fig. 1.—Principal localities mentioned in text account of *Cisticola chiniana*. 1. Arusha. 2. Chimala. 3. Dar-es-Salaam. 4. Dodoma. 5. Iringa. 6. Kidodi. 7. Kilimanjaro. 8. Kilosa. 9. Kipangere Range. 10. Lake Manyara. 11. Lake Natron. 12. Lake Nyasa. 13. Lake Rukwa. 14. Lake Tanganyika. 15. Lake Victoria. 16. Loliondo. 17. Mbeya. 18. Mombasa. 19. Mwanza. 20. Same. 21. Serronea River. 22. Shinyanga. 23. Tabora. 24. Tura. 25. Uluguru Mts. 26. Usambara Mts.

A careful reading of the ranges attributed to Tanzanian races of *C. chiniana* by White (1962) and Britton (1980) reveals a large area of the interior of the country missing from any of the range descriptions. Judging from the map of the species' range in Hall and Moreau (1970), part of this gap in range descriptions may reflect an actual lack of records of occurrence, but neither White nor Britton assigns any subspecies to the area southeast of Tabora, where the species does indeed occur. Britton's account seems to suggest that *chiniana* is replaced in the Iringa District of south-central Tanzania by *Cisticola njombe*, but this is true only in the southernmost part of the District, where *njombe* is confined to higher elevations than those reached by *chiniana* in this area. It appears that *njombe* is limited to a

rather restricted habitat, and its relationships are uncertain. Although other recent authors had considered it nearest to *C. lais*, Hall and Moreau (1970) tentatively listed it as forming a superspecies with *C. chiniana*. Britton (1980) stated that *njombe* forms "a superspecies with the allopatric *C. chiniana*," but his concept of superspecies must differ from the usual one, as he placed 12 other species of *Cisticola* between *chiniana* and *njombe*. In the most recent treatment of the genus, Traylor (1986) reverts to placing *njombe* near *lais* rather than *chiniana*. It is doubtful that any sort of competitive exclusion is involved in the relative distributions of *chiniana* and *njombe* in south-central Tanzania.

The ranges given by Lynes are not precisely outlined, but it appears as if the birds from all of central Tanzania should be *fischeri*. However, a series of 27 specimens from the vicinities of Dodoma and Iringa (BM[NH], YPM, CM) indicates that there is a population occupying an area in central Tanzania that differs from *fischeri* in having seasonal plumages. I am indebted to M. A. Traylor, Jr., for calling my attention to an easily overlooked statement by Lynes (1934b). Referring to a series taken at Iringa (BM[NH]), Lynes stated only "The *Cisticola* Review requires correction in respect of *fischeri's* mode of dress"; by this he meant that some of the Iringa specimens, taken in November, were molting, demonstrating that this population does in fact have seasonal plumages, whereas he had attributed the perennial mode to *fischeri* in his 1930 monograph. However, Lynes was mistaken in considering this population to be typical of *fischeri*. I have examined specimens of *fischeri* from elsewhere in its range taken during the months of December through August, and find no seasonal differences other than those attributable to normal wear and fading. Although the "summer" plumage of the birds in the Dodoma/Iringa series is indistinguishable from that of *fischeri*, the "winter" plumage is highly distinctive, and matched in no other population of the species. The BM(NH) series clearly shows that the prealternate molt into "summer" plumage begins in mid-November. Unfortunately no specimens are available from this area taken later than 6 March or earlier than 20 August, the period during which the prebasic molt must take place (see beyond for mention of a worn 20 May specimen from the putative eastern edge of the range of the central Tanzanian race). August and September specimens in the type series are relatively lightly worn.

It may seem to some that a population recognizable during only part of the year should not be given a subspecific name, but a little contemplation will aid in recalling that there is ample precedent among migratory temperate species; the population of *Cisticola chiniana* differs strikingly from these in that it is the Basic rather than the Alternate Plumage that is distinctive. This population of central Tanzania may be called:

***Cisticola chiniana keithi*, new subspecies**

*Holotype*.—CM 146864, adult male, from 50 miles N of Dodoma, Dodoma (formerly Central) Province, Tanzania, collected 10 September 1960 by A. C. Twomey and John Williams (field no. 2559).

*Diagnosis*.—Inseparable from *C. c. fischeri* (*sensu* Lynes, 1930) in Alternate ("summer") Plumage. Basic Plumage unlike Alternate Plumage, nearest to the "perennial" (Basic) plumage of *C. c. ukamba* of the highlands of Kenya and northeastern Tanzania, but decidedly paler. The edges of the mantle feathers, tertials, and wing coverts are not merely paler but buffier, less gray. The crown is paler, with black streaks more sharply defined. The pale buff superciliary line

is distinct (obsolete or absent in *ukamba*). The tail is paler and of a more reddish brown, and the flanks and a pale wash across the lower breast are of a yellower, less grayish buff. In the distinctness of the crown streaking, *keithi* resembles *humilis* rather than *ukamba*, but the crown is otherwise much paler than in *humilis*.

*C. c. keithi* differs most distinctly from the coastal race *heterophrys*, which is a dark, plain-backed form with no streaks on the crown and, in some individuals only, barely discernible blurry streaks in the centers of the dark gray-brown mantle feathers.

There is some noticeable individual variation among the 9 relatively unworn August–September specimens. CM 146844 has the mantle edgings (but not those of the wing feathers including the tertials) more rufescent, approaching those of *procera*, and also has the broadest black mantle streaks. The crown is darkest in YPM 93258 (which also has the grayest edges to the dorsal feathers), palest in CM 146754. The holotype and CM 146844 have the greatest development of the narrow black crown streaks; in YPM 93260 they are almost invisible. Collectively, however, these specimens do not differ *inter se* any more than series of other subspecies, from which they are clearly differentiated.

*Range*.—Central Tanzania; see *Remarks* for intergradation with adjacent subspecies.

*Etymology*.—It is a pleasure to dedicate this new subspecies to G. Stuart Keith of the American Museum of Natural History, my mentor in African ornithology.

*Remarks*.—Eastern Tanzania is occupied by the distinctive *C. c. heterophrys*. A coastal series from Mombasa (the type series in CM) and Diani, Kenya, to Dar-es-Salaam, Tanzania, is quite uniform. The subspecies is not confined to the coastal plain, however. Two specimens from 6200 ft at Lukwangule, southern end of the Uluguru mountains (BM[NH]) and seven specimens (MCZ, BM[NH], USNM) from Kilosa, just west of the Ulugurus and about 225 km SE of the type locality of *keithi*, differ only slightly from the coastal series. They are slightly paler and brighter on the crown, paler and less grayish (more rufescent) on the back, and paler and more reddish brown on the tail. This can be interpreted as a tendency toward *keithi*, but the Kilosa series shows no indication of the marked dorsal streaking so characteristic of *keithi*. On the other hand, two specimens (UMMZ 157561-2) from Kidodi (ca. 160 km E of Iringa, ca. 95 km S of Kilosa) appear to illustrate intergradation with *keithi*. Both Traylor and Storer have annotated the label of UMMZ 157561 as *heterophrys*; it is indeed closest to this race as typified by the type series from Mombasa in CM, with dorsal streaking only slightly better defined than in extreme specimens of *heterophrys*. UMMZ 157562, however, was annotated by Storer as “too streaked for *heterophrys*” and identified as *fischeri* by Traylor. It is a very worn 20 May bird and does, indeed, resemble that race, but from its southern locality it is more plausibly interpreted as representing the eastern limit of *keithi*, which, at that time of year, would be expected to be in worn Alternate Plumage and inseparable from the perennial plumage of *fischeri*.

Farther north, a series from Same (YPM), about the same distance inland as Kilosa and also separated from the coast by mountains (the Usambaras), is *ukamba*, with no suggestion of introgression from *heterophrys*; the coastal plain at this latitude is much narrower than that east of Kilosa.

A single 3 August specimen from the north end of Lake Manyara (UMMZ 94961) is particularly interesting. It is just completing a molt into a plumage in which the crown and back are much like that of the late August specimens of



*keithi*. The tertials, however, instead of being black with sharply contrasting buff edges (varying in degree of rufescence) as in the Basic Plumage of *keithi*, have less intensely black centers, and the edgings are darker and less contrasting. In this respect they resemble those of the perennial plumage of *fischeri* and Alternate Plumage of *keithi*, in that they are not intensely black and the edgings show little contrast, but the latter are distinctly warmer, less gray in color in the Manyara bird than in *fischeri*. Lake Manyara is an area where intergradation between *keithi* and *fischeri* might be expected. Two 26 January LACo specimens are labeled "E. side Lake Manyara, 60 mi So. of Arusha." This locality is difficult to interpret, as Lake Manyara is approximately 60 miles *west*, not south of Arusha. These two specimens are typical of *fischeri* in appearance. Both are moderately worn, and both are initiating a molt on the throat. There is no molt at this time of year in *keithi* (specimens still in worn alternate plumage as late as early March), and Lynes (1930) stated that, at Tabora (ca. 120 km E of Tura, the type locality of *fischeri*), the months of June through September "seem to more or less cover the general moulting period." On the other hand, BM(NH) 1933.6.11.119, from Ndembezi, Sinyanga [=Shinyanga], ca. 210 km N of Tura, 23 December 1933, was annotated by Lynes on 10 October 1934 as "(nearly ad.) ♂ completing m.[oult] to first S.[ummer plumage]". Clearly there is much yet to be learned about the molts of *Cisticola chiniana*, especially in areas where subspecies typified by seasonal plumages, such as *keithi*, may intergrade with those having only a perennial plumage, such as *fischeri*.

I have seen no specimens from areas of Tanzania where intergradation between *keithi* and *procera* to the south or southeast might be expected.

A series of 8 specimens from the vicinity of Mbeya, southwesternmost Tanzania (between Lake Rukwa and the Kipengere Range at the north end of Lake Nyasa, where the map in Hall and Moreau [1970] shows a gap in the range of *chiniana*; see map in Ripley and Heinrich 1966, where the lake is spelled "Rukwe") cannot be assigned to any known race of *Cisticola chiniana*. White (1962) included "South-west Tanganyika (Rukwa)" in the range of *C. c. fortis* Lynes; this is based on his earlier brief footnote (White, 1960), which reads, in its entirety: "*C. c. fortis* occurs at rukwa [*sic*]; one specimen examined since writing this note." I have been unable to discover where this specimen is housed. Britton (1980) assigned "SW Tanzania between Lakes Rukwa and Tanganyika" to *fortis*. It is not clear whether this was taken on White's authority (based on one specimen), or additional specimens seen by Britton or one of his collaborators. In any case, the Mbeya series is utterly unlike *fortis* specimens taken at the same time of year in inland Angola, where the type locality of *fortis* lies. The Mbeya series is most closely related to *keithi* and *fischeri*. Lake Rukwa is so close to the collecting localities of the YPM series as to make it difficult to believe that two such different races of *chiniana* can be found so close together. There are two possible explanations. One is that White erred in extending the range of *fortis* as far east as Lake Rukwa. I cannot believe, however, that White would have identified as *fortis* a Rukwa specimen that resembled the Mbeya series. An alternative explanation is that *fortis* is, as originally described by Lynes (1930), a full species, overlapping in range with *C. chiniana* subsp. in the vicinity of Lake Rukwa. Certainly *fortis* is distinct in appearance; it differs from *all* races of *chiniana* in having the white of the underparts greatly reduced, with the gray area of the sides and flanks more extensive medially, even meeting or almost so across the breast (suggested in Lynes's plate 11). It completely lacks streaks on the back, resembling in this respect

the geographically distant *C. c. heterophrys*. The latter, however, has the typical *chiniana* amount of white on the underparts, and also has a fairly distinct superciliary line, lacking in *fortis*. The differences between *fortis* and the possibly sympatric population of *chiniana* are much greater than between *fortis* and *heterophrys*. Against the theory that *fortis* is not a race of *chiniana* is the later paper of Lynes (1934a:24), in which, after extensive experience with *fortis* in the field, he stated “. . . now that it is known in life, [it] proves to be no more than a race of *chiniana*. There is no mistaking the *chiniana* behavior of the bird . . .” Writing of the two plain-backed forms *fortis* and *heterophrys* in relation to streaked-backed races of *chiniana*, Traylor (letter of 6 November 1986) stated that “people who know them in the field consider them identical behaviorally.” It is obvious that White’s (1960) statement about the gap in southwestern Tanzania of our knowledge of the forms of *Cisticola chiniana* is still largely true; clearly more collecting needs to be done. Meanwhile, the distinctive population represented by the YPM series may be called:

***Cisticola chiniana mbeya*, new subspecies**

*Holotype*.—YPM 93268, adult male just completing prealternate molt. Collected ca. 20 mi ENE of Mbeya, Southern Highlands Province, Tanzania (elevation 1800 m), 28 December 1962, by Gerd Heinrich (field no. 36151).

*Diagnosis*.—“Summer” (=Alternate) plumage similar to those of *keithi* and *fischeri* dorsally, but averaging slightly darker, especially on the crown. Underparts in general purer white, without buffy wash. Sides and flanks much grayer, with buff tinge confined to posteriormost flanks. “Pectoral patch” of Lynes (1930) (a darker pigmented area near the anterior end of the pigmented sides, extending farther medially) more prominent. Differs from *procera*, the next race to the southeast, in being much less rufescent dorsally, including crown, back, wing edgings, and tail; dorsal streaks much heavier, flanks grayer, and pectoral patch more prominent. All of the series of *mbeya* is in late stages of the molt, and several, including the holotype, have a few worn feathers remaining that indicate that this race has a bright “winter” plumage like that of *keithi*, and does not exhibit the “perennial mode” of Lynes.

*Range*.—Known only from the vicinity of Mbeya and Chimala, Southern Highlands Province, southwestern Tanzania (elevation 1400–1800 m).

*Etymology*.—Named for the type locality.

***Apalis jacksoni***

White (1962) recognized only two subspecies of this species, the nominate race and the distinctive *A. j. bambuluensis* Serle from the Bamenda highlands of Cameroon. Traylor (1986) also admitted *A. j. minor* Ogilvie-Grant for the isolated population from the lowlands of southern Cameroons; this race was also recognized by Bannerman (1953) and by Mackworth-Praed and Grant (1973), although the latter authors apparently did not examine specimens; Louette (1981) followed White in considering the Cameroon lowland population inseparable from nominate *jacksoni*. I have not been able to examine specimens to verify the alleged narrower black throat patch of *minor*, but the measurements presented by Ogilvie-Grant (1917) in his original description certainly suggest that *minor* is indeed significantly smaller than *jacksoni*, with (in small series) no overlap in either wing or tail measurements.

The population of northern Angola was described by Meise (1958) as *A. j. albimentalis*, characterized as having more white on the chins of females and



generally lighter color (but with deeper golden underparts). Traylor (1962) compared two adult males, an adult female, and a juvenile from Angola with four males and seven females from Kenya, and found the only difference between the two series to be slightly darker, more greenish (not deeper gold) underparts in the Angola males. He later (Traylor, 1986) formally synonymized *albimentalis* with nominate *jacksoni*. I have examined the two females from N'Dalla Tando, Angola, in the AMNH collection, the same specimens mentioned by Chapin (1953:297); three of the four FMNH Angola specimens seen by Traylor (1962); and a series of three adult males and four adult females from YPM; see Ripley and Heinrich (1966) for localities and map. This is a larger series of Angola specimens than has been assembled by any previous worker. Comparison of these specimens with an ample series from East Africa indicates that *albimentalis* is a recognizable subspecies, although the alleged character that gave it its name is not valid. In both sexes (especially in males), the underparts of Angola birds are brighter yellow (*contra* Traylor) than in those of East Africa, with less invasion toward the midline of the duskier color of the flanks. The throat patch (black in males, gray in females) extends slightly farther caudad, especially in females; depending on preparation, this gives the appearance of the yellow of the breast extending slightly farther anteriorly on each side of the throat patch. The green of the dorsum of Angola specimens is distinctly brighter and yellower (less grayish) in both sexes. The gray crown of Angola males is paler than in Kenya *jacksoni*, but little different from that of Uganda males (see beyond); the crown color of females is paler than in either Kenya or Uganda specimens. The extent of the black or blackish face mask is variable in both sexes.

Like so many other African highland birds, *Apalis jacksoni* has isolated populations in Kenya and in western Uganda and adjacent Rwanda and Burundi (see Hall and Moreau, 1970: map 216). The western birds differ in series from true *jacksoni* of Kenya and eastern Uganda (type locality Mt. Elgon) as follows:

Males: crown, wing coverts and tertials paler gray, less blackish; black facial mask averaging less extensive, generally not extending above eye, whereas the eye is completely surrounded by black in Kenya males; dorsum slightly brighter, yellower green.

Females: difference in color of crown, wings and back less noticeable but present; the area of the male's mask (ear coverts to lores) tending to be uniform with the crown rather than contrastingly blacker.

Color of the underparts is too variable to permit its use in identifying individual specimens, but there is a tendency in Kenya males for the duskier color of the flanks to expand toward the midline, reducing the amount of pure yellow.

The characteristics of the western Uganda specimens strongly suggest an approach to *albimentalis* of Angola. However, a series of eight males and one female from Baraka, west of northern Lake Tanganyika, Zaire (AMNH), is not the same as the form from western Uganda, but is, if anything, even darker than Kenya *jacksoni*. Chapin (1953:297) has already commented briefly on this series.

It is apparent that Traylor's and especially White's treatment of *Apalis jacksoni* is oversimplified, and that a full scale revision, bringing together all available material from throughout the range of the species, is highly desirable.

### *Apalis porphyrolaema*

White (1962) and Traylor (1986) synonymized *Apalis affinis* Ogilvie-Grant, from Ruwenzori, with the nominate race from the Kenya highlands, but it was recognized as a valid race of *porphyrolaema* by Jackson (1938) and Chapin (1953:

287). The only color character mentioned for *affinis* has been its darker reddish-brown throat patch. Comparison of the composite AMNH/CM series of three adults and one juvenile from Ruwenzori with 19 adults and two juveniles of *porphyrolaema* from Kenya supports recognition of *affinis*; an even better character than the throat patch is the color of the gray underparts—much paler (whiter) in *affinis*, thus accentuating the slightly darker throat. There is no discernable difference in the color of the upperparts.

CM 145902, an adult female, was collected on 3 August 1960 by A. C. Twomey and John Williams in the Impenetrable Forest, Kigezi, Uganda. It is a typical example of *affinis*, extending the known range of that subspecies slightly to the south.

### *Apalis cinerea*

Several Fernando Poo endemic subspecies are also resident on Cameroon Mountain, on the adjacent mainland. Bannerman (1939) specifically stated that this was not true of *Apalis cinerea sclateri* (Alexander). He considered specimens from Cameroon Mountain to be the same as *A. c. cinerea* (Sharpe) from East Africa (type locality Mt. Elgon). Those from elsewhere in Cameroon he identified as *A. c. funebris*, a supposedly dark race that he had described himself three years earlier. Serle (1950) compared a series of 30 skins from "British Cameroons" with the BM(NH) material, including types, of *cinerea*, *funebris*, and *sclateri*. He showed that "*funebris*" was based on a worn, dirty holotype, and that his new series of topotypes was not separable from *cinerea*. He called all Cameroon birds *A. c. cinerea*, and in this he was followed by White (1962), Louette (1981), and Traylor (1986). Of Searle's 30 specimens, however, only one was from Cameroon Mountain. As he stated that there was considerable variation in his series in the amount of buff on the underparts and in the shade of brown on the head, it is highly likely that the distinctiveness of his solitary non-inland specimen escaped him.

The Carnegie Museum of Natural History has two specimens of *Apalis cinerea* (CM 106345, 106362) from Buea, on the slope of Cameroon Mountain. These are completely outside the range of variation in the combined CM and AMNH East African series of 87 *A. c. cinerea*. On the other hand, they agree exactly with AMNH 598672 from Fernando Poo (*sclateri*) in the intensity of buff color on the underparts, and in having the crown much grayer, less brown, resulting in less contrast between the crown and the slate-gray black. In most East African specimens, the area below the eye from the ear coverts to the base of the bill is noticeably blacker than the crown, resulting in a masklike appearance. This is much less conspicuous in the two Buea and one Fernando Poo specimens.

After the above comparisons were made at AMNH, I examined two specimens from the FMNH, taken at 5900 ft elevation on Cameroon Mountain. These are somewhat intermediate, but are clearly closer to *sclateri* than to *cinerea*. FMNH 95803 has the heavily pigmented underparts typical of *sclateri*, but in the contrast of brown cap with gray back it approaches *cinerea*. FMNH 95802 is less heavily pigmented below, matching a few extreme specimens of *cinerea*, but has the grayish, non-contrasting cap of *sclateri*. As in the Buea and Fernando Poo specimens, there is little or no indication of a dark facial mask at the lower edge of the brown cap.

On the basis of the specimens examined, I have no hesitation in assigning the

Cameroon Mountain population of *Apalis cinerea* to *A. c. sclateri* and not to the nominate race.

### *Sylvietta leucophrys*

Chapin (1953) and other authors have generally recognized two subspecies of this little warbler of montane forests. The populations of the Kenya highlands and easternmost Uganda (type locality Mt. Elgon, on the Kenya/Uganda border) and that of the Ruwenzori Mountains of the Uganda/Zaire border are assigned to the nominate race. The name *S. l. chloronota* Hartert (type locality forest NW of Baraka, near Lake Tanganyika, Zaire) is used for the populations from "Mountains west of Lake Edward, the Kivu Volcanoes, and highlands of Kigezi District, south to the vicinity of Baraka and to the Kungwe-Mahare highlands east of Lake Tanganyika" (Chapin, 1953:252). In addition, White (1962) and Traylor (1986) considered the well-marked *S. chapini* Schouteden of the Lendu Plateau, Zaire, which lacks the distinctive white superciliary of *S. leucophrys*, as a subspecies of the latter species. Study of the combined AMNH/CM series of 62 skins of *Sylvietta leucophrys* (excluding *chapini*) indicates that some modification needs to be made in the range statements.

Specimens of this species from the areas attributed to *S. l. chloronota* by Chapin (1953:252) are by no means uniform. The subspecies is generally said to be characterized by a greenish rather than brown dorsum, and by having the brown of the postocular line extending downward on the cheeks. The latter character is not as consistent as is back color. In Kenya specimens of *leucophrys* the postocular line is variable, but usually rather broad. In about one-third of the specimens, the adjacent cheeks are slightly stained with brown. Among six topotypes of *chloronota* from Baraka, the postocular line is broad, with a variable extension of brown onto the cheeks. The two specimens with the least development of this character state could be matched with extreme examples in the Kenya series. There is an additional, previously unmentioned character for distinguishing *chloronota* and *leucophrys*. In the latter, the posterior flanks are pale gray, contrasting abruptly with the greenish yellow under tail coverts. In *chloronota* the gray of the flanks is much mixed with greenish on the posterior half of the body, leading to the color of the under tail coverts.

Typical *chloronota* occurs from Baraka north, west of Lake Tanganyika, the Ruzizi River, and Lake Kivu. As mentioned by Chapin (1953:252), a specimen he collected at 8100 feet on Mt. Nyemilima, northwest of Lake Edward, is referable to *chloronota*. However, two AMNH specimens from "Kagera, Kivu, 2400 m" and one from "NW slope Mt. Millens, Kivu Distr., 7900'," appear to be intergrades between the two subspecies. The highly variable series from Kigezi (4 AMNH, 4 CM), an area attributed to *chloronota* by Chapin, must also be considered to be intergrades, a status already suggested by the fact that Stuart Keith and John Williams independently labeled their specimens as "*chloronota*" in quotation marks.

A series of nine specimens collected by W. Doherty from October 1900 to March 1901 (AMNH) at "Escarpment, Kikuyu Mts., 8000-9000'," appears to differ from other Kenya material of *leucophrys* in being very heavily instead of lightly washed with brown on the underparts. However, they are poorly made, understuffed skins and are apparently stained, so the significance of this color

difference is dubious. Specimens from nearby Molo do not differ from those from other localities in Kenya.

As mentioned above, the population of this species in the rather isolated Ruwenzori range has been attributed to the nominate race. A series of nine specimens from Ruwenzori and the nearby Mpanga Forest shows that this population, not unexpectedly, is separable from *leucophrys*. It may be called:

*Sylvietta leucophrys arileuca*, new subspecies

*Holotype*.—CM 145398, adult female, from the Mpanga Forest, Fort Portal, Toro, Uganda, elevation 5000 feet, collected 20 July 1960 by A. C. Twomey and John Williams (field no. 1094).

*Diagnosis*.—Differs from both nominate *leucophrys* and *chloronota* in having a much broader superciliary line, which is pure white rather than slightly stained with brownish (especially at the posterior end), and extends farther posteriorly. The underparts are paler and purer gray than in any other population, and the midabdominal area is pure white or nearly so rather than the same gray as the rest of the underparts. The back color is somewhat variable, but tends to be closer to the greenish of *chloronota* than to the brown of *leucophrys*. The postocular line is narrow; all but one of the eight adult specimens have this line narrower than in any other specimens examined.

The CM series includes 7 specimens of *leucophrys*, 4 of *leucophrys-chloronota* intergrades, and 3 of *arileuca* that have soft-part color annotations on the labels. The bills of the *leucophrys* series are annotated as "flesh-brown" (J. Williams) or "grey horn" (A. Forbes-Watson). The intergrades are annotated as "dark horn, lower mandible flesh" or "flesh-horn, lower mandible paler" (Williams). The *arileuca* specimens are labeled "bill horn [or dark horn], lower mandible flesh-white" (Williams). The dried bills of the *leucophrys* series support the lack of mention on their labels of a paler lower mandible, and the *arileuca* series has the palest bills of all; even the one specimen whose upper mandible is described as "dark horn" has *both* mandibles paler than those of any of the *leucophrys* or *leucophrys-chloronota* intergrade series. It appears likely that a paler bill is another subspecific character of *arileuca*.

*Range*.—Known only from the Ruwenzori range on the Zaire/Uganda border and the nearby Mpanga Forest, south of Fort Portal, Toro, Uganda.

*Etymology*.—From the Greek, *ari-*, meaning very, and *leukos*, meaning white, referring to the broad white superciliary line and white midabdomen that characterize this subspecies.

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## SPERGENASPIS: A NEW CARBONIFEROUS TRILOBITE GENUS FROM NORTH AMERICA

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### ABSTRACT

A new trilobite genus, *Spergenaspis*, is erected based upon three Mississippian trilobite species from the midcontinent of the United States. Two of the species, *S. easleyi*, new species, from the Chouteau Formation of Missouri, and *S. salemi*, new species, from the Salem Limestone of Indiana are previously undescribed. The third species, *S. mauvaisensis* (Hessler) is reassigned from the genus *Richterella* and is known from the Upper Osagean or Lower Meramecian of Illinois.

Known occurrences of *Spergenaspis* suggest that species of this genus inhabited similar environmental settings. Lithologies from which *Spergenaspis* is recovered vary from sandy lime packstone to oolitic to crinoidal lime grainstone. Interpreted depositional environments for these lithologies include transgressive shallow subtidal and sand shoal.

### INTRODUCTION

Hessler (1965) erected the Mississippian trilobite genus *Richterella* and based it on three species known from the midcontinent region of North America. One of these species, *Richterella mauvaisensis* Hessler, differs from the diagnosis of the genus in that it exhibits considerably less vaulting with a bell-shaped glabella, possesses a broad concave-up frontal area, lacks a straight section in the facial sutures from  $\epsilon$  to  $\zeta$ , and possesses a distinct subdivision of the pygidial ribs into anterior and posterior bands. Recent recognition of two previously undescribed Mississippian trilobite species bearing characters similar to *R. mauvaisensis* Hessler justifies their being grouped together as a distinct genus, *Spergenaspis*. These features, which characterize *R. mauvaisensis* Hessler, can best be grouped under the subfamily Linguaphillipsiinae as outlined by Hahn and Hahn (1972).

Members of the trilobite subfamily Linguaphillipsiinae are not known from the Lower Carboniferous of North America even though they are relatively widespread geographically and stratigraphically in Europe and Asia (Hahn and Hahn, 1973, 1982; Engel and Morris, 1975; Brauckmann, 1978; Kobayashi and Hamada, 1980). Assignment of the new genus *Spergenaspis* to the subfamily Linguaphillipsiinae marks the first documentation of this subfamily in North America. Moreover, recovery of a species of *Spergenaspis* from the base of the Chouteau Formation (Middle Kinderhookian) indicates that immigration into North America was concomitant with the Kaskaskia onlap (Brezinski, 1986a). That these representatives have previously gone unnoticed may be the result of either their scarcity or their paleoecology. The latter of these two possibilities will be discussed below.

Terminology utilized in this paper is similar to that proposed by Harrington (1959) and Richter and Richter (1949). Specimens illustrated in this study are deposited at The Carnegie Museum of Natural History (CMNH). Type specimens

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of *Spergenaspis mauvaisensis* (Hessler) examined for this study are reposit with the Illinois Geological Survey.

#### STRATIGRAPHIC DISTRIBUTION

The known species of *Spergenaspis* are found in Middle Kinderhookian through Lower Meramecian strata in the midcontinent region of the United States. The oldest species, *Spergenaspis easleyi*, new species, was recovered from the basal strata of the Chouteau Formation (Middle Kinderhookian) of central Missouri (locality 1 of Brezinski, 1986a). Canis (1968) found that these strata are assignable to the *Siphonodella quadruplicata*-*S. crenulata* conodont zone, which is roughly equivalent to the Cu II<sub>a</sub> ammonoid zone of Tournaisian rocks of Europe. The next youngest species, *Spergenaspis mauvaisensis* (Hessler), was found in Upper Osagean or Lower Meramecian strata of Scott County, Illinois (see Hessler, 1965, for locality information). The youngest species, *Spergenaspis salemi*, new species, was collected from several localities in the Salem Limestone (Meramecian) of southwestern Indiana. Additionally, two pygidia, from the Keokuk Limestone (Osagean) of St. Genevieve County, Missouri, tentatively assigned to the genus *Waribole* by Brezinski (1986b), are here reassigned to the new genus.

#### PALEOECOLOGY

Although *Spergenaspis* exhibits a considerable stratigraphic range, its restricted geographic distribution parallels many other trilobite genera known from this time interval. As a result, Kobayashi and Hamada (1980) were able to discern several distinct trilobite realms composed of numerous provinces. One of the most distinct of these faunal provinces is the midcontinent area of North America, where no less than 10 of 18 known genera are endemic. Studies by Brezinski (1986a, 1986b) indicate that this endemism is the result of trilobite genera becoming narrowly adapted to specific environmental conditions, thus precluding emigration to other areas which might not provide the precise conditions necessary for habitation. This niche-specialization is indicative of stenotopic species (Valentine, 1972).

All presently known occurrences of *Spergenaspis* appear to be found in rocks that represent similar environmental settings. *S. easleyi* from the Chouteau was recovered from a sandy wackestone lithology which is interpreted as having been deposited in a shallow subtidal transgressive environment (King, 1980; Brezinski, 1986a). Coarse tuberculate ornament on several of the associated trilobite species may indicate agitated conditions (McNamara and Fordham, 1981). The lithology in which *S. mauvaisensis* (Hessler) occurs, is a coarse-grained crinoidal packstone with lenses of crinoidal grainstone, also suggestive of high-energy conditions of deposition. *S. salemi* was recovered from a poorly cemented, coarse-grained, oolitic, gastropod grainstone which Donahue (1967) interpreted as having been formed in a sand-bar shoal environment. The two pygidia of the undetermined species of *Spergenaspis* from the Keokuk Limestone of Missouri were collected from well-sorted crinoidal lime grainstones associated with oolitic grainstone strata. These occurrences of *Spergenaspis* indicate that members of this genus probably inhabited high-energy environmental settings such as shoal sands or nearshore tidal sands, although some transport is probable. The low relief and lack of surface ornamentation shown by members of this genus may be the result, in a large part, of their ecological affinities. Similar features are exhibited by trilobite species from the Gilmore City Limestone of Iowa (Kinderhookian-Osagean). The Gilmore City Limestone, like the examples discussed above, consists



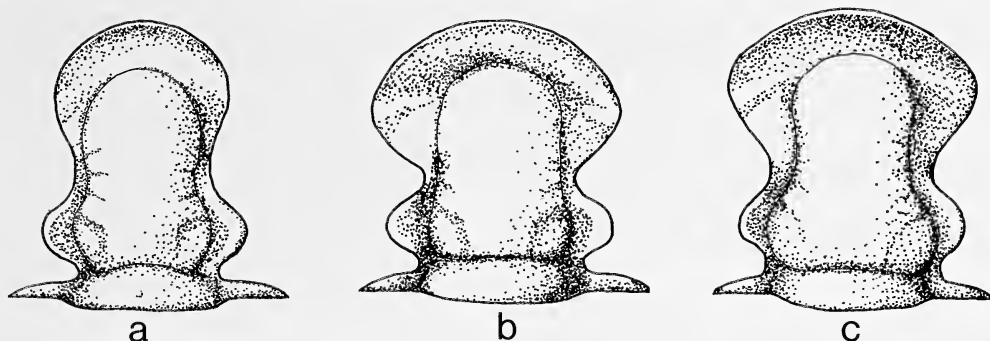


Fig. 1. — Comparative reconstructions of cranidia of a, *Spergenaspis easleyi* new genus and new species; b, *Spergenaspis salemi* new genus and new species; c, *Spergenaspis mauvaisensis* (Hessler), all approximately  $\times 3.5$ .

of an oolitic grainstone of shoal-water origin. The lack of surface features, and low profile to the exoskeletons of these species are interpreted as adaptations to reduce friction created by passing currents, thus making them more hydrodynamically stable.

#### SYSTEMATIC PALEONTOLOGY

Family Proetidae Salter, 1864

Subfamily Linguaphillipsiinae Hahn and Hahn, 1972

Genus *Spergenaspis*, new genus

*Type species.* — *Spergenaspis salemi*, new genus and new species.

*Other species assigned.* — *Spergenaspis easleyi*, new genus and new species, *Spergenaspis mauvaisensis* (Hessler, 1965).

*Diagnosis.* — Smooth isopygous genus with cranidium possessing a broad concave-up fixigena, bell-shaped glabella, broader behind  $\gamma$  than in front of it, and large palpebral lobes, located at the base of the glabella. Pygidium smooth with wide border flange; ribs divided by pleural furrow into bands of equal width.

*Comparisons.* — Genera similar to *Spergenaspis* and with which it might be confused are *Waribole* Richter and Richter, 1926, *Gitarra* Gandl, 1968, *Linguaphillipsia* Stubblefield, 1948, *Pseudowaribole* Hahn and Hahn, 1967, and *Griffithidella* Hessler, 1965. *Waribole* can be distinguished from *Spergenaspis* in that the former possesses a conical glabella lacking a constriction at  $\gamma$ , more anteriorly located eyes, and narrower palpebral lobes. A somewhat similar genus *Linguaphillipsia* can be differentiated from *Spergenaspis* by the greater anterior elongation of the glabella, more anterior location of the palpebral lobes, by the much smaller width to length ratio of the pygidium, by the commonly well-developed surface sculpture, and structure of the pygidial ribs on the former. The genus *Gitarra* differs from *Spergenaspis* in that the former has a more strongly constricted, guitar-shaped glabella, very large eyes, and a shorter, broader pygidium with well-defined segmentation and ribs that extend to the margin. *Spergenaspis* differs from *Pseudowaribole* (*Pseudowaribole*) in that *Spergenaspis* is isopygous, lacks a well-defined border furrow to the cephalon, has more posteriorly located (with respect to the glabella), larger, palpebral lobes, stronger constriction of the glabella at  $\gamma$ , and a longer and broader pygidium possessing a well-defined border. *Spergenaspis* differs from *Pseudowaribole* (*Geigibole*) in that the latter is not

isopygous, exhibits a very short and broad, subtriangular pygidium, a broad cranidium, much larger, more anteriorly located palpebral lobes and eyes, and a narrower anterior fixigenae. Pygidia of *Griffithidella depressus* var. *depressus* (Girty) (see Hessler, 1965, pl. 38, figs. 1-11, 14) are quite similar in many characteristics to those of *Spergenaspis*. Inasmuch as no cranidia of *G. depressus* var. *depressus* are known, it is questionable whether these pygidia are truly assignable to the genus *Griffithidella*.

***Spergenaspis salemi*, new genus and new species**

Fig. 2A-I, M

*Holotype*.—An incomplete cephalon from the Salem Limestone at a railroad cut near Spergen Hill, Washington County, Indiana. NW  $\frac{1}{4}$ , SE  $\frac{1}{4}$ , sec. 24, T2N, R4E, Salem Quadrangle. Collected by R. T. Garney. CMNH 34433.

*Paratypes*.—An external mold of a cranidium and two pygidia from the Cleveland Quarry, Monroe County, Indiana. SE  $\frac{1}{2}$ , NW  $\frac{1}{4}$ , sec. 20, T7N, R4E, Clear Creek Quadrangle. Collected by H. B. Rollins. 1 cranidium and 6 pygidia from the Spergen Hill railroad cut collected by R. Garney. CMNH 34434-34437.

*Diagnosis*.—Species of *Spergenaspis* with a subcylindrical glabella, slightly wider at the base than at  $\gamma$ , palpebral lobes very large, anterior facial sutures recurved from  $\gamma$  to  $\beta$ . Pygidium semicircular in outline.

*Description*.—Cephalon semicircular in outline, very low in relief and vaulting. Glabella approximately 1.50 times as long as the maximum width, subcylindrical and rounded anteriorly, widest between the eyes, tapering slightly to the 3 p glabellar furrow, then nearly parallel sided to faintly diverging anteriorly. 1 p furrow broad, shallow, and nearly obsolete, all other glabellar furrows very faint to obsolete on the dorsal exoskeleton. Occipital lobe of nearly even width only slightly wider at axis. Occipital furrow narrow and arcuate, becoming shallower near the axial furrow. Palpebral lobes large and crescentic in outline, located very near the base, with the 1 p furrow intersecting the dorsal furrow anterior to the palpebral midline (longitudinal). Facial sutures strongly divergent from  $\gamma$  to  $\beta$ , broadly rounded through  $\beta$ . Preglabellar field gently concave-up (sagittal) to flat (exsagittal). Eyes narrow and near vertical, reniform. Border becomes more concave-up anteriorly, extends posteriorly onto a short sharp genal spine which is 0.33 times the total librigenae length.

Pygidium low in relief and semicircular in outline, 1.48 to 1.61 times as wide as long. Axis 0.37 times as wide as maximum pygidial width, composed of 12 to 13 smooth rings. Ring furrows become increasingly obscure and shallow near the posterior terminus. Pleural fields mildly convex, composed of 6 to 9 ribs, the posterior two of which are difficult to discern on the dorsal surface, but are evident on the internal surface. Each rib exhibits an anterior and posterior moiety of nearly equal width. Pleural furrows terminate at the border. Border from 0.20 to 0.28 the total pygidial length (sagittal), broader near the posterior terminus and becoming narrower anteriorly.

*Discussion*.—Similarity in morphology suggests that *Spergenaspis salemi* is closely related to *Spergenaspis mauvaisensis* (Hessler). This is especially evident in the overall plan to the cephalon and pygidium, but differs in several respects. Firstly, *S. mauvaisensis* (Hessler) has a straight diverging section on the anterior facial sutures from  $\gamma$  to  $\beta$ , more acutely rounded facial suture at  $\beta$ , a bell-shaped glabella which is relatively wider between the eyes and more constricted at the base and  $\gamma$ . The pygidium of *S. mauvaisensis* is more parabolic in outline and possesses a smaller width to length ratio. *Griffithidella depressus* var. *depressus* (Girty) exhibits similar numbers of rings and ribs as *S. salemi*. However, it can be differentiated from the latter by the slightly shorter, broader pygidial outline and the poorly defined border.

*Age and distribution*.—Known only from the Salem Limestone, Meramecian, of southern Indiana.

*Etymology*.—This species is named for the Salem Limestone from which the type material was collected.

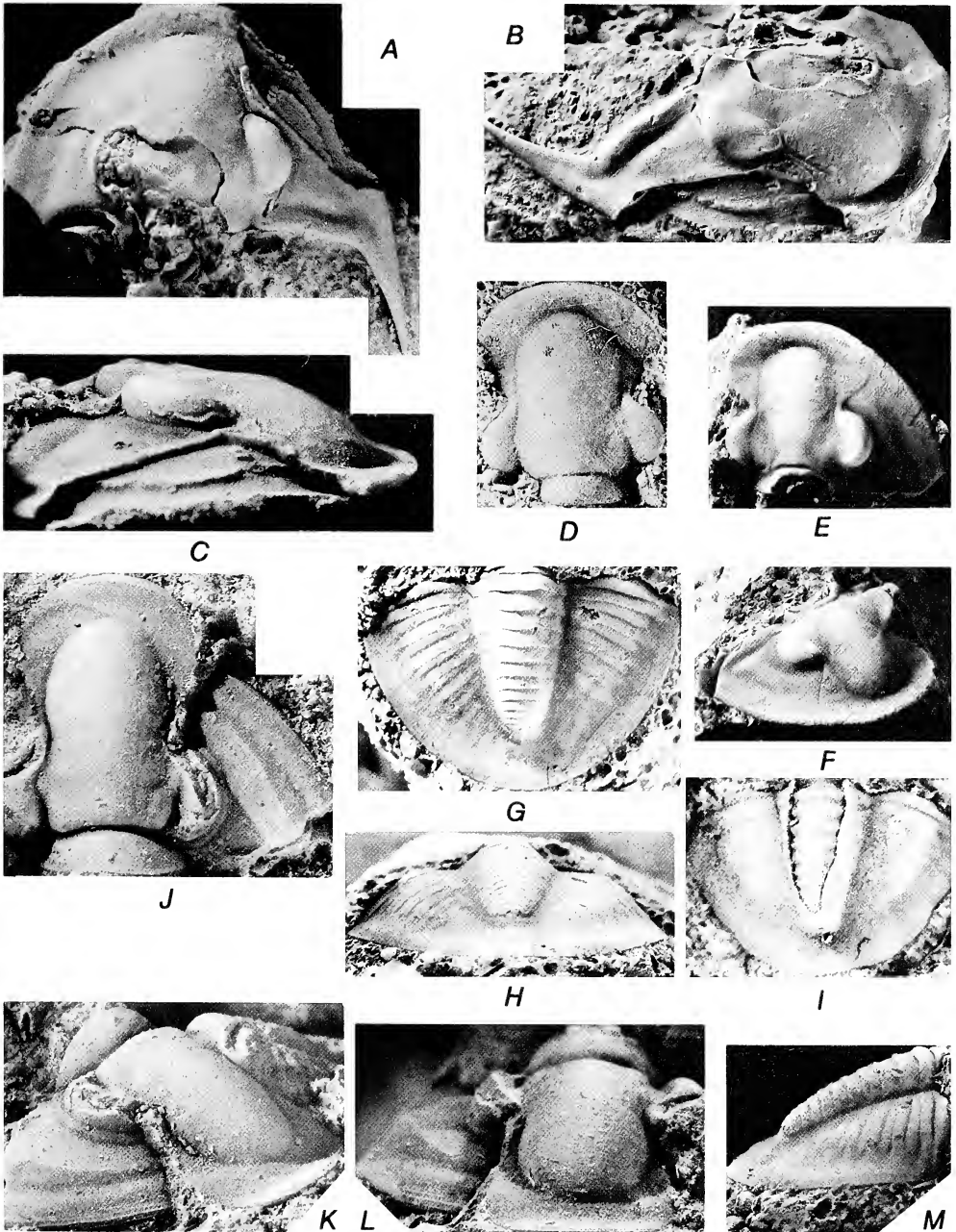


Fig. 2.—A–I, *Spergenaspis salemi* new genus and new species. A–C, dorsal, oblique, and lateral views of partially exfoliated holotype cephalon, CMNH 34433,  $\times 4$ ; D, external mold of paratype cranidium, CMNH 34434,  $\times 3$ ; E, F, dorsal and oblique views of unexfoliated paratype cephalon, CMNH 34435,  $\times 2.5$ ; G, H, M, dorsal, posterior, and lateral views of paratype pygidium, CMNH 34436,  $\times 3.5$ ; I, partially exfoliated paratype pygidium, CMNH 34437,  $\times 3$ . J–L, *Spergenaspis easleyi* new genus and new species, dorsal, oblique, and anterior views of unexfoliated holotype cephalon, CMNH 34438,  $\times 5$ .

*Spergenaspis easleyi*, new genus and new species  
Fig. 2J–L

*Richterella?* sp. BREZINSKI, J. Paleont. 1986, 60:873, table 1, fig. 5.

*Holotype*.—A partial cephalon from the basal Chouteau Formation 1.75 km northwest of Easley, Missouri along the bluffs of the Missouri River, collected by the author, 1980; CMNH 34438.

*Other material*.—Only the holotype is known.

*Diagnosis*.—Species of *Spergenaspis* with a narrow (transverse) cranidium, glabella narrower at  $\gamma$  and the base than between the eyes. Frontal glabellar lobe semicircular in outline, anterior facial sutures only slightly divergent, rounded from  $\gamma$  to  $\beta$ ,  $\gamma$  narrower than  $\epsilon$ .

*Description*.—Profile of cephalon low. Glabella smooth and elongate, 1.76 times as long as maximum width, constricted at  $\gamma$ , frontal glabellar lobe broadly rounded. Glabellar furrows, except 1 p, very faint, nearly obsolete, 1 p furrow shallow and faint, intersects dorsal furrow at the anterior half of the palpebrae, extends posteriorly at an oblique angle to the axis, then forms an obtuse angle and intersects the occipital furrow at nearly a right angle. Frontal glabellar lobe descends gently into a concave preglabellar field which is upturned to the margin (sagittal) and becomes flattened to downsloping (exsagittal). Palpebral lobes relatively large and crescentic, located at the base of the glabella. Occipital lobe broad and smooth, widest at the axis, very gently downsloping into a narrow, sharp occipital furrow with an arcuate trace. Eyes not well preserved on holotype, but appear to be vertical and reniform. Librigenae gently downsloping from the eyes becoming more steeply inclined onto the border then descending less steeply to the margin. Facial sutures moderately divergent from  $\gamma$  to  $\beta$ , broadly rounded from  $\gamma$  to  $\alpha$ .

*Discussion*.—Although it is generally inadvisable to propose new species on the basis of a single specimen, *S. easleyi* is so markedly differentiable from either *S. salemi* or *S. mauvaisensis* the erection of a species in this case seems warranted. The narrow, anteriorly elongate glabella, which is constricted at  $\gamma$ , appears to be a synapomorphic character connecting this genus with ancestral Linguaphillipsiinae such as *Pseudowaribole*.

*Age and distribution*.—Known only from the type locality in the basal Chouteau Formation (Middle Kinderhookian) of Boone County, Missouri.

*Etymology*.—Named for the town of Easley in Boone County, Missouri near where the holotype was collected.

#### CONCLUSIONS

The subgenus *Spergenaspis* arose during or immigrated into North America concurrently with the Kaskaskia transgression. Representatives have probably previously gone unnoticed primarily because: 1) they are not common where they do occur, 2) they are highly restrictive with respect to the type of environment in which they are found. This type of habitat restriction may also be the main reason for the strong endemism exhibited by this genus, inasmuch as members may have been unable to emigrate owing to unfavorable conditions outside their local habitat.

#### ACKNOWLEDGMENTS

The holotype and several of the paratype specimens of *Spergenaspis salemi* were collected by Ronald T. Garney from the Spergen Hill locality. Jack Donahue and H. B. Rollins made available additional bulk samples from the Cleveland Quarry. Lois Kent of the Illinois Geological Survey loaned the type material of *Spergenaspis mauvaisensis* (Hessler). J. H. Stitt, J. F. Taylor and C. A. Kertis made many helpful suggestions to improve earlier drafts of this manuscript. Dr. C. Brauckmann provided information as to the possible taxonomic assignment of the three species herein assigned to *Spergenaspis*.

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## CONTENTS

- Art. 15. Decompression syndrome in fossil marine turtles  
..... **Bruce M. Rothschild** 253
- Art. 16. Towards a postglacial history of the northern Great Plains: A  
review of the paleoecologic problems .....  
**Cathy W. Barnosky, Eric C. Grimm and H. E. Wright, Jr.** 259
- Art. 17. Fossil crab (Decapoda: Brachyura) fauna from the Late  
Cretaceous (Campanian-Maastrichtian) Pierre Shale in Bowman  
County, North Dakota .....  
**Annette B. Tucker, Rodney M. Feldmann, F. D. Holland, Jr.**  
**and Kenneth F. Brinster** 275
- Art. 18. Excavations at the Harney Site slave cemetery, Montserrat,  
West Indies ..... **David R. Watters** 289
- Art. 19. Description of skeletal remains from a Black slave cemetery  
from Montserrat, West Indies ..... **Robert W. Mann,**  
**Lee Meadows, William M. Bass and David R. Watters** 319

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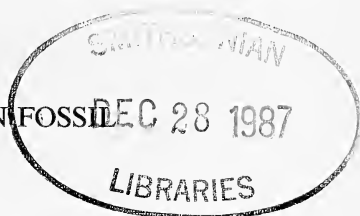
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**THE CARNEGIE**  
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DECOMPRESSION SYNDROME IN FOSSIL  
MARINE TURTLESBRUCE M. ROTHSCILD<sup>1</sup>

Research Associate, Section of Vertebrate Fossils



## ABSTRACT

Avascular necrosis of bone occurs in Tertiary and Quaternary marine turtles, as it does in Cretaceous mosasaurs. Assessment for potential underlying pathophysiology suggests decompression syndrome as the etiology of this bone pathology. The pathophysiology of decompression syndrome, and predisposing and protective factors are reviewed.

## INTRODUCTION

Avascular necrosis of the humeral head results in loss of viability (death) of bone. The devitalized bone often becomes necrotic and liquefied, subsequent to the loss of vascular supply, so that the stresses of normal use result in fracture of the surviving subchondral bone (Resnick et al., 1981; Feldman et al., 1981). The result of such fractures is discrete collapse of the articular surface. This complication of decompression syndrome, which has been observed in man, was recently discovered in Cretaceous mosasaurs (Rothschild and Martin, 1987). The present report describes avascular necrosis in Cretaceous marine turtles and Cenozoic marine and freshwater Chelonians.

## METHODS

Cretaceous marine turtle specimens in the collection of the University of Kansas Museum of Natural History were examined for avascular necrosis of the humeral head, as evidenced by focal subsidence (e.g. collapse) of the articular surface. Specimens were also examined in the Institut Royal des Sciences Naturelles des Belgique (Brussels, Belgium), the Red Mountain Museum (Birmingham, Alabama) and the Auburn University Museum (Auburn, Alabama). Specimens found to have focal subsidence of the humeral articular surface were sectioned for confirmation of avascular necrosis. A simple coronal cross-section was adequate for examination. The sections were subjected to radiologic and electron probe analysis and to bright field, polarizing, fluorescent, and scanning electron microscopic examination. Polarizing and fluorescent microscopy of the sections revealed trabecular patterns, the disruption of which characterize avascular necrosis. Scanning electron microscopy revealed ultrastructure alterations, and permitted precise placement of the electron probe utilized for bismuth analysis. Standard ionization chamber technique was utilized for assessment of radiation levels.

## RESULTS

Examination of Cretaceous marine turtles contemporary with the mosasaurs revealed a specimen of *Desmatocheles* (Desmatochelyidae) manifesting avascular necrosis (Table 1) of the humeral heads. This was seen as focal subsidence within the articular surface of the intact specimen (Fig. 1A) and by collapse of the necrotic zone as seen in cross section (Fig. 1B). Evidence of avascular necrosis was also found in both Eocene (*Eosphargis*: Dermochelyidae and Cheloniidae, species indet.) and Oligocene (*Oligochelone* and Cheloniidae, species indet.) turtles. Avascular necrosis was also present in *Porthochelys* (Toxochelyidae), and *Protostega*

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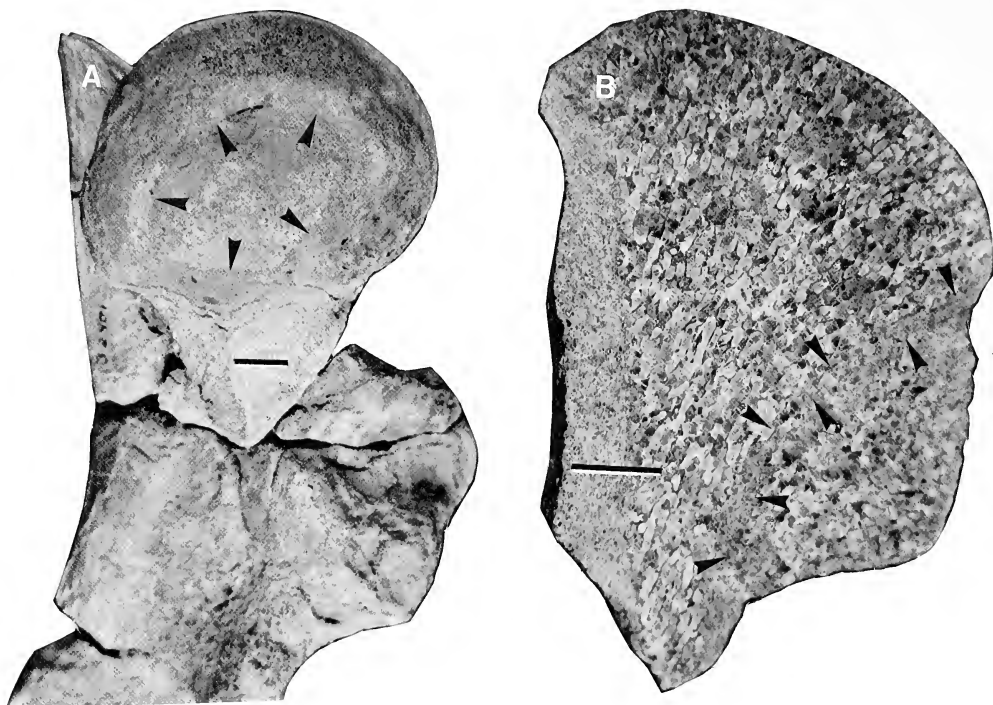


Fig. 1.—*Desmatochelys* humerus showing A, focal subsidence on articular surface of head (arrows) and B, collapsed necrotic zone in cross-section of head.

*dixie* (Protostegidae) the Cretaceous. Avascular necrosis was not observed in *Psephophorus*, *Lytoloma*, and *Trionyx*, although only limited numbers of humeri were available for examination. Microscopic examination of sectioned material revealed only focal linear loss of definition of trabeculae and collapse of subchondral bone. Trabecular architecture was intact and normal extrinsic to the zone of involved bone. Electron probe analysis revealed no evidence of significant bismuth exposure. Radiation levels in affected and unaffected specimens were similar.

#### *Avascular Necrosis in Turtles*

Avascular necrosis is an easily recognized pathology, characterized by the appearance of articular surface collapse. Its presence is confirmed in 11% of fossil Cheloniidae examined and in four other marine turtle families (Table 1). The differential diagnosis of avascular necrosis in turtles is as previously reported for mosasaurs: radiation poisoning, bismuth poisoning, and decompression sickness (Rothschild and Martin, 1987). Lack of variation in radiation levels and absence of bismuth as determined by electron probe analysis suggest decompression sickness as the etiologic factor. As *Protostega* shared a common habitat with the mosasaurs, (evidenced by mosasaur bite lesions in a *Protostega* carapace (RMM 2255) in the Red Mountain Museum collection), it is possible that *Protostega* was subjected to the same pathophysiologic mechanism in development of avascular necrosis as the mosasaurs. Sudden changes in depth (e.g. rapid surfacing), possibly

Table 1.—Incidence of avascular necrosis of turtle humeral heads.

Taxon	Epoch	Specimens examined	Frequency %
Cheloniidae			
<i>Caretta caretta</i>	Holocene	8	0
<i>Oligochelone rupeliensis</i>	Oligocene	9	11
species indet.	Oligocene	3	33
species indet.	Eocene	15	7
Toxochelidae			
<i>Porthochelys laticeps</i>	Cretaceous	1	100
<i>Ctenochelys</i> cf. <i>tenuitesta</i>	Cretaceous	1	0
species indet.	Cretaceous	3	0
<i>Lytoloma gosseleti</i>	Eocene	2	0
Protostegidae			
<i>Protostega dixie</i>	Cretaceous	2	50
Desmatochelyidae			
<i>Desmatochelys</i> sp.	Cretaceous	4	50
Dermochelyidae			
<i>Psephophorus rupeliensis</i>	Oligocene	2	0
<i>Eosphargis gigas</i>	Eocene	4	50
Testudinidae			
species indet.	Pleistocene	9	0
Trionychidae			
<i>Trionyx levalensis</i>	Eocene	3	0

related to escape from mosasaurs or other predators, may have played a major role in the development of the lesions.

### Decompression Syndrome in Non-Turtle Vertebrates

Decompression syndrome is commonly thought of as a phenomenon dependent upon breathing an exogenous air supply, but this requirement is not absolute. Decompression illness has also been noted in man subsequent to breath-holding dives (Pauley, 1965; Kooyman et al., 1973; Strauss, 1970). Repeated two minute dives of 20 to 40 m have resulted in the decompression syndrome (Kooyman et al., 1973). Pauley (1965) reported neurologic manifestations of decompression syndrome in man after sixty 15 to 20 m dives performed over a five hour period. The decompression syndrome etiology was confirmed by the "dramatic response" of symptomatology to recompression. Pauley (1965) also reported three similar cases occurring after 20 "bottom drops" during Norwegian escape-tank training. Polynesian (Tuamotu) pearl divers manifest an intriguing dichotomy of susceptibility to decompression illness. Those who performed 40 to 50 two minute dives to greater than 30 m, with three to four minutes between dives, or who participated in vigorous 4 to 5 hr diving sessions to 50 m developed decompression illness (Pauley, 1965; Strauss, 1970). Those who maintained at least ten minute intervals between dives (a different "diving habit" pursued at an adjacent island) did not develop decompression syndrome. The Ama (Japanese diving women), who dive to more shallow depths or maintain a longer surface interval, are apparently unaffected by decompression disease (Anderson, 1966; Strauss, 1970).

Decompression syndrome has also been documented in other vertebrates. Berk-

Table 2.—*Physiological mechanisms promoting vertebrate protection from decompression syndrome (derived from Anderson, 1966; Denison et al., 1971; Strauss, 1970).*

---

Decreased lung surface area for gas exchange
—Small lung volume
—Thoracic wall collapse
—Exhalation prior to descent
—Cartilage/muscle airway support (minimizes air trapping)
Augmented, targeted circulation
—Intracardiac blood shunting
—Increased intravascular volume
—Increased hematocrit
—Decreased red blood cell size
—Elasticity of blood vessels and sinuses
—Anuria-water conservation
—Vasoconstriction (e.g. of muscle beds)
Protection from hypothermia
—Decreased ratio of surface area to mass
Metabolic
—Decreased activity of
—histamine
—serotonin
—bradykinin
—smooth muscle acting factor
—Altered complement activation

---

son (1967) reported the death of a seal from decompression syndrome after forced surfacing from 300 m. Gas bubbles have been noted in blood samples obtained from diving birds at various depths. After four dives to 4 atm of pressure, nitrogen tension is increased to two to four times the original; after four dives to 7.8 atm nitrogen pressure increased to five times the basal value. After 2.5 minutes of submersion nitrogen increased from 82.4 to 89.5% of total gases (Kooyman et al., 1973). Most vertebrates avoid decompression syndrome only because of the briefness of their dives (Kooyman et al., 1973), but decompression syndrome can and does occur with prolonged submergence in a variety of vertebrate taxa.

The pathophysiology of decompression syndrome is more complex than simple vascular occlusion by nitrogen bubble emboli. Major causative factors may be hemoconcentration and red blood cell agglutination, resulting in decreased tissue perfusion (Strauss, 1970). Risk factors (derived from Strauss, 1970) for development of decompression syndrome include dehydration, fatigue, increased hemoconcentration, stress, impaired circulation, hypothermia, systemic disease, injury, and obesity.

Physiological protective mechanisms are listed in Table 2. However, the impact of the protective mechanisms is not straightforward. For example, the polycythemic (increased packed red blood cell content of blood) response may in some instances actually reduce circulation due to its effect on blood viscosity (Lutz and Bentley, 1985).

### *Decompression Syndrome in Turtles*

Berkson (1967) first identified decompression syndrome in turtles. He reported that blood drawn from turtles under pressure forms bubbles in the syringe and

further noted the gas emboli death of a turtle after rapid decompression from 18.7 atm. Berkson also noted that turtle blood was supersaturated with respect to nitrogen at a given atmospheric pressure and that stepwise decompression also produced caisson disease (decompression sickness). The susceptibility of turtles to decompression syndrome is further substantiated by the observation of avascular necrosis, a phenomenon previously noted in mosasaurs and attributed to decompression syndrome (Rothschild and Martin, 1987).

While diving habits of some turtles are known, the impact on turtles of these risk and protective factors during diving has been the subject of limited study. The leatherback turtle (*Dermochelys coriacea*) is known to dive almost continuously with short surface intervals and can dive to 475 m. *Lepidochelys olivacea*, the olive ridley sea turtle, can dive to 300 m (Eckert et al., 1986). The loggerhead turtle (*Caretta caretta*) utilizes its lungs as a major oxygen storage system and spends only 1% of its time on the surface (Lutz and Bentley, 1985). Some turtles, such as *Pseudemys scripta* (Glass and Wood, 1983), have significant cutaneous respiration which could conceivably protect them from decompression sickness; 65% of the total CO<sub>2</sub> elimination in *Trionyx mucita* is non-pulmonary.

There is evidence that some of the physiological protective mechanisms may be non-operative in turtles. Lutz and Bentley (1985) noted that turtles inhale prior to dives, enhancing their risk. Lung collapse does occur in turtles at 80–160 m (Berkson, 1967), which leaves a substantial range of depth in which gas exchange continues.

Avascular necrosis has been identified in *Desmatocheles*, *Prostostega*, *Porthochelys*, *Oligochelone*, *Eosphargis*, and several indeterminate Cheloniidae. Factors which might affect susceptibility to this phenomenon, apparently related to decompression syndrome, include depth of dives, time at depth, surface time, lung type, cutaneous respiration, complement responses to micro-bubble formation, and perhaps even nitrogen excretion in the form of ammonium carbonate (Strauss and Sampson, 1986).

A general survey of contemporary turtle humeri would allow identification of susceptible species. Correlation of occurrence of avascular necrosis with diving habits, risk factors, and protective mechanisms in extant turtles may allow assessment of the relationship between risk factors and protective mechanisms.

#### ACKNOWLEDGMENTS

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TOWARDS A POSTGLACIAL HISTORY OF THE NORTHERN  
GREAT PLAINS: A REVIEW OF THE  
PALEOECOLOGIC PROBLEMS

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Assistant Curator, Section of Paleobotany

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## ABSTRACT

Central to the late Quaternary ecological and cultural history of the northern Great Plains is an understanding of (1) the nature and magnitude of vegetational and climatic change during the last glaciation, when the Pleistocene megafauna went extinct, and (2) the timing and extent of aridity in the early or middle Holocene, when populations of bison and humans apparently were reduced. Limited pollen data suggest that during full glacial time the eastern half was covered with spruce parkland, while the western half was probably treeless. The difference persisted through late glacial time, when an open forest of spruce and hardwoods developed in the east and grassland in the west. During the Holocene, the timing of Altithermal warmth and aridity is poorly documented, as is the response of the biota, yet the east/west contrast is well demarcated. Sites in the eastern sector commonly show middle Holocene warming and dryness typical of the Midwest, whereas western sites register maximum drought in the early Holocene. The variable response is best explained as a metasynchronous shift from a glacial climate influenced by the ice sheet to one governed by the early Holocene maximum in summer radiation. The protracted presence of Laurentide ice delayed the radiation response in the east, whereas "upwind" of the ice sheet, warming and drought were registered early.

## INTRODUCTION

Two major trends have dominated the environmental history of the northern Great Plains since the late Pleistocene. The first occurred between 18,000 and 10,000 yr B.P. at the close of the last glaciation, when the amelioration of climate significantly altered the biota and landscape. With the retreat of the Laurentide and Cordilleran ice sheets, a vast region was available for colonization by plants, animals, and humans. Upon this landscape new communities formed, composed of those species that had survived outside the ice border. The composition of late glacial communities is not well known, but it undoubtedly resulted from a combination of factors, including the prevailing climate, the distribution of suitable substrates, the ability of species to take advantage of freshly exposed surfaces, and the rate at which plant populations were able to migrate from unknown refuges. The environment was clearly favorable for large herbivores, which were abundant on the plains at this time. The heyday of the megafauna, however, ended abruptly, either as a result of environmental and climatic change or at the hands of big-game hunters of the Clovis culture (see Martin and Klein, 1984).

The second paleoenvironmental trend was towards increased dryness and warmth in the early and middle Holocene (the Altithermal), followed by greater effective

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moisture and cooling in the late Holocene. This climatic change is well documented in the Far West and Midwest, but on the Great Plains the details of the climatic signal and vegetational response are poorly known, as are the attendant adjustments in human and animal populations.

Understanding the kind, timing, and magnitude of the late Pleistocene and Holocene vegetational and climatic changes of the northern Great Plains is important in solving some current problems in archeology, paleoclimatology, and biogeography. Among these are the controversy over the extinction of the Pleistocene megafauna as well as the nature of Holocene cultural history. The purpose of this paper is to present the available paleoecologic data, to compare the post-glacial environment in different regions, and finally to clarify the paleovegetational and paleoclimatic questions that still need to be answered. The northern Great Plains is defined here as the region bounded by the Rocky Mountains on the west, the Nebraska Sandhills on the south, the Prairie Coteau on the east, and (arbitrarily) the Canadian border on the north.

### THE PLEISTOCENE-HOLOCENE TRANSITION

For the vast area from the eastern Dakotas to the western edge of the plains in Montana and Wyoming—a distance of 1500 km—almost no published paleobotanical data exist to indicate whether forest, tundra, or steppe prevailed during the glacial period and when and how grassland came into existence. Because of this absence of data, inferences must be drawn from sites peripheral to the northern Great Plains. The only information on full glacial vegetation is the record of *Picea* forest in northeastern Kansas at Muskotah Marsh and Arrington Marsh (see Fig. 1 for location of sites), which lie southeast of the Nebraska Sandhills and 250 km southwest of the ice margin (Grüger, 1973). This full glacial forest differed from the modern boreal forest of central Canada by the absence of *Pinus banksiana*.

By the time ice lobes in Iowa and the Dakotas had reached their maxima about 14,000 yr B.P. (Clayton and Moran, 1982), *Picea* had begun to spread its range northward into the Des Moines area (Baker and Waln, 1985). By 12,000 yr B.P., spruce forest was replaced along its southern margin by prairie in southern South Dakota. This transition is recorded at the Rosebud site, an interdunal depression at the northern edge of the Nebraska Sandhills, 175 km southwest of the ice margin (Watts and Wright, 1966). About 11,000 yr B.P., *Quercus*, *Populus*, *Fraxinus*, and other hardwoods, which were probably confined to the central United States in glacial time (Jacobsen et al., in press), expanded their ranges northward and mixed with *Picea* in the eastern part of the northern Great Plains and the Midwest. This admixture of trees has no close analogue in the present-day, but the vegetation is presumed to have been open and dominated by spruce, with some hardwoods but no pine. The western limit of the forest is not known. At two sites in the glaciated region of northeastern South Dakota (Pickerel Lake: Watts and Bright, 1968; Medicine Lake: Radle, 1981), deciduous trees replaced *Picea* about 11,000 yr B.P. before prairie developed at 10,000 yr B.P. Pollen data from east-central North Dakota (Woodworth Pond: McAndrews et al., 1967; Seibold site: Cvangara et al., 1971) indicate a similar sequence. Farther north in Canada, *Picea* forest was succeeded directly by prairie about 10,000 yr B.P. at the Hafichuk, Riding Mountain, Herbert, Scrimbit, Glenboro, Sewell, and Russell sites (see Ritchie, 1976). At Cottonwood Lake in central South Dakota, late glacial *Picea* forest gave way to a parkland of *Populus* and *Picea*, with *Fraxinus nigra*, minor other hardwoods, *Artemisia*, Poaceae, and other herbs about 12,000 yr

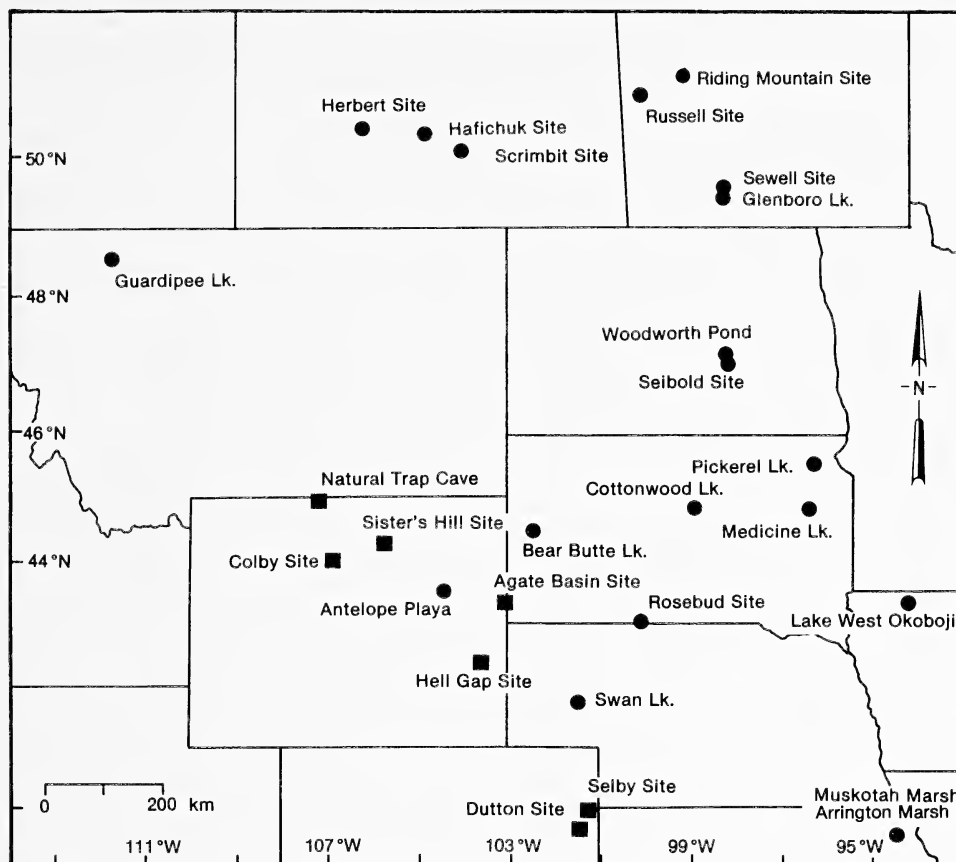


Fig. 1.—Location of sites discussed in text. Circles indicate sites with fossil pollen records; squares show the location of archeological/paleontological sites.

B.P. Parkland, in turn, was replaced by prairie at about 10,000 yr B.P. (E. C. Grimm, unpublished data; Fig. 2).

Thus, for the eastern Great Plains the pollen records suggest that open spruce forest with some deciduous trees existed in late glacial time. This forest followed the ice retreat northward into southern Manitoba and Saskatchewan. Farther south, forest was replaced by prairie and parkland in southwestern and central South Dakota and by deciduous forest in the eastern Dakotas. A wedge of deciduous forest apparently extended westward as far as Woodworth in central North Dakota, bounded by prairie on the southwest and spruce forest on the north and northeast. This wedge seems to resemble the zone of deciduous forest that now occurs between prairie and conifer forest in northwestern Minnesota, but unfortunately only a preliminary pollen diagram is available from the Woodworth site (McAndrews et al., 1967), and it lacks radiocarbon dates. With continued warming and drying, the band of deciduous forest disintegrated, and spruce forest gave way directly to prairie as far north as southern Canada.

To the west of the Great Plains, late glacial vegetation is inferred mainly from high-altitude sites of glacial origin. Upper treeline in the northern Rocky Moun-

**COTTONWOOD LAKE**  
**Sully County, South Dakota**  
**Analyst: E.C. Grimm**

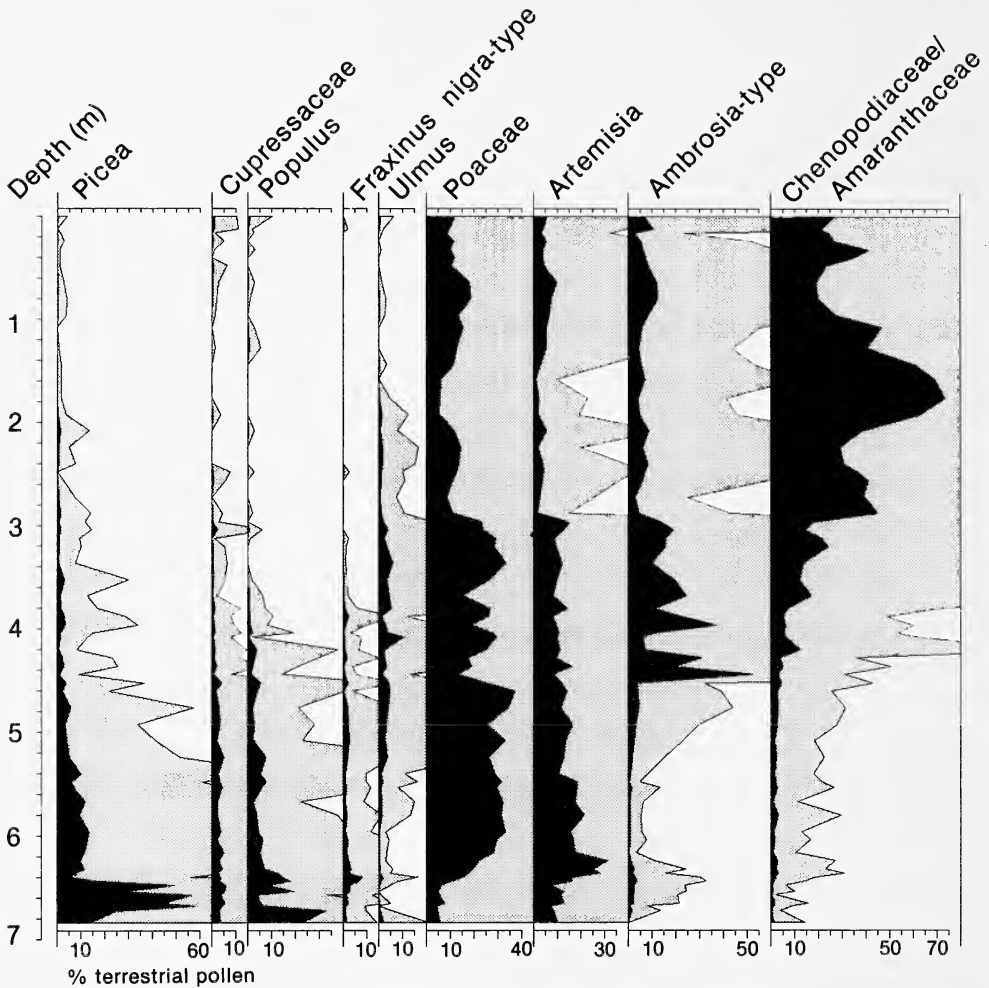


Fig. 2.—Pollen percentage diagram for selected taxa from Cottonwood Lake, South Dakota. Core segment 6.38–6.48 m has a radiocarbon date of  $13,410 \pm 120$  (WIS-1626), which is judged 1000–3000 years too old based on age determinations at other Dakota sites (see discussion in text). The erroneous date is presently attributed to an incorporation of ancient carbon into the sediments from glacial till.

tains was lowered by at least 1000 m during the last glaciation, and high elevations were probably covered by alpine tundra or steppe vegetation (Baker, 1983; Barnosky et al., in press). Although the location of montane conifers during glacial time is unclear, they expanded their range rapidly throughout the Rocky Mountains between 11,000 and 9000 yr B.P. The early appearance of present-day forest communities and the general uniformity of the late glacial forest from one mountain range to another argues against great latitudinal or elevational displacement

of conifer forests in glacial time. A more reasonable scenario is that conifers grew in small populations along the lower mountain slopes during glaciation, bounded by tundra or steppe at higher and lower elevations. The geomorphic evidence of permafrost and strong winds in the Great Plains near the ice margin and on the high plains of Wyoming also suggests that the lowlands were largely treeless (Mears, 1981; Péwé, 1983; Kutzbach and Wright, 1986).

In the northwestern Great Plains, Guardipee Lake in western Montana seems to corroborate the inferences drawn from montane sites (C. W. Barnosky, unpublished data). The site lies in the area of the former Two Medicine glacial lobe, which originated in the Rocky Mountains and advanced 65 km eastward onto the plains, terminating only a few kilometers from the Laurentide ice sheet (Alden, 1932; Lemke et al., 1965). The pollen data indicate treeless vegetation for the past 12,000 years or so (Fig. 3), and the ratio between percentages of *Artemisia* and Poaceae suggests grassland prior to 11,400 yr B.P. as opposed to sagebrush steppe. By contrast, a contemporaneous record from Marias Pass 35 km to the west implies parkland of *Picea* and *Abies* in the mountains (Carrara et al., 1986). The high percentages of *Pinus* pollen in the late glacial sediments at Guardipee are similar to present-day values, and pine pollen was probably blown from distant sources, just as today. Unfortunately, the Guardipee record is not old enough to reveal whether conifers were on the plains during full glacial time. If trees were indeed present beforehand, it could be argued that their elimination occurred with the onset of greater seasonal contrasts and windier conditions in the late glacial, when the Cordilleran and Laurentide ice sheets parted and allowed cold polar air to funnel down the Alberta corridor onto the Montana plains. The influence of an ice-free corridor on the climate, however, must have been short-lived, because pollen types diagnostic of tundra are not present at Guardipee Lake. Also, by 11,400 yr B.P. the Two Medicine lobe had retreated west of the Continental Divide (Carrara et al., 1986).

Two other sites in the western sector suggest an unforested landscape in the late glacial period. Antelope Playa, a 13,000-yr record from the Powder River Basin of eastern Wyoming, features *Artemisia*-dominated vegetation during both late glacial and Holocene times, with no evidence of trees (Markgraf and Lennon, 1986). Bear Butte Lake just east of the Black Hills records open parkland vegetation in the late glacial interval, succeeded by prairie in the Holocene (E. C. Grimm, unpublished data). At this site, the presumed (but undated) late glacial period of open vegetation is dominated by *Artemisia* and Poaceae. *Picea* pollen amounts to about 10%, and *Pinus* is absent. Later, percentages of *Picea* pollen decline and *Pinus* appears, marking the Holocene immigration of pine into the nearby Black Hills. Coincident with this transition, herbaceous pollen types change in character, with *Ambrosia* and Chenopodiaceae/Amaranthaceae becoming dominant.

#### EXTINCTION OF THE PLEISTOCENE MEGAFaUNA

Vertebrate records of glacial age are equally sparse on the northern Great Plains, although those that have been studied are generally consistent with the environmental reconstructions based on pollen data. Assemblages from Natural Trap Cave (Martin and Gilbert, 1978; Gilbert and Martin, 1984) and the Colby Site (Walker and Frison, 1980) in the Bighorn Basin of north-central Wyoming show similarities with late Pleistocene faunas of interior Alaska, which imply a steppe-tundra vegetation. However, they also contain alpine-tundra elements not found

in the Alaskan assemblages (Chomko and Gilbert, 1987). Graham and Mead (in press) discuss some of the specific differences between Alaska and Wyoming faunas. *Saiga*, *Lemmus*, and *Mammuthus primigenius*, while common in Alaska, were absent in Wyoming. Conversely, the Wyoming faunas contain taxa, including *Perognathus*, *Cynomys*, and *Thomomys*, that do not occur in the Alaska faunas. Not surprisingly, the glacial faunas from Wyoming are more similar to those from sites along the former ice sheet margin in the Dakotas, Nebraska, and western Iowa than those from interior Alaska (Graham and Mead, in press). Considered as a whole, the late Pleistocene faunas from these northern plains sites suggest increasing grasslands and aridity towards the west (Graham and Mead, in press; R. W. Graham, personal communication, 1987), as do the pollen data.

This reconstruction does not seem to apply farther south. From the occurrence of typically montane species in the fauna of the Hell Gap site, Roberts (1970) argues for a late glacial forest on the plains of southeastern Wyoming. Hoffman and Jones (1970) believe that the present occurrence of montane species in the Black Hills indicates a once forested connection with the mountains to the west. The early Holocene fauna at the Agate Basin site, in the short-grass prairie just southwest of the Black Hills, contains species that today occur in boreal and montane forests, including those of high altitudes in the Black Hills, as well as species typical of steppe (Walker, 1982). Thus a parkland of forest and grassland is indicated. Paleosols at the Agate Basin site, the nearby Sheaman site, and the Sister's Hill archeological site in the Powder River Basin in northeastern Wyoming all indicate conditions wetter than present in the early Holocene (Reider, 1982a, 1982b, 1983). Faunas from the Selby and Dutton sites in northeastern Colorado indicate a grassland environment prior to 12,000 yr B.P. and a subsequent trend towards increased moisture (Graham, 1981). From a survey of vertebrate fossil sites in the western plains, Graham (1981) concludes that grassland prevailed until about 11,000 yr B.P., but from then until 8000 yr B.P. the area was probably forested.

A study of the Waubonsie local fauna from southwestern Iowa suggests that extinction of the grazing megafauna may have come with the collapse of the mixed grassland and open forest in the eastern Great Plains (Rhodes, 1984). This site, dated at about 14,600 yr B.P., yielded 23 taxa of small mammals that together suggests greater microhabitat diversity in the area than at present. Cold-steppe taxa predominate, but the presence of temperate/mesic mammals implies isolated areas of conifer and deciduous trees (Rhodes, 1984).

Proponents of the climatic hypothesis of megafaunal extinction argue that the late Pleistocene spruce forest was a greater food resource than the modern closed boreal spruce forest of Canada, because openings provided a nutritious ground flora that grazing and browsing animals could utilize. In addition, at the end of the Pleistocene the rapidity of climatic change and the resultant disruption of plant communities throughout the continent prevented large mammals from adapting their physiological and behavioral patterns to new conditions (Guthrie, 1984). Many animals became extinct, and others were much reduced in range (muskox). Some that survived developed smaller body size (bison). Other survivors had been minor components before but were favored by the environmental change and increased in relative numbers (moose). It is well established that late Pleistocene faunas in the Great Plains, as elsewhere on the continent, were composed of assemblages that have no analogues today; the local faunas contained species that are now allopatric (Graham and Lundelius, 1984). One inference is

that the vegetation was not so strongly zoned as it is today but rather was characterized by a mosaic pattern that allowed animals to utilize a variety of vegetation types without travelling long distances. Guthrie (1984) postulates that such a mosaic pattern was particularly favorable for the non-ruminant herbivores, which had to rely on a varied diet in order to obtain proper nutrition. Their relatively simple digestive system could not handle toxins that accumulate in plants during the growing season. Non-ruminants thrive in a climate with low seasonal contrasts, that is, one with a long period of spring plant growth, when nutrient contents of the plants are high and toxins low. It was these non-ruminant mammals that became extinct (for example, horse, mammoth, mastodon, ground sloth, rhinoceros, camelids), while the ruminants survived (caribou, deer, moose, wapiti, bison). This scenario for megafaunal extinctions puts much of the burden of support on the change in vegetational patterns at the end of the Pleistocene. It is possible, however, that the sympatry in animals was not widely shared by the plants—making human predation a more likely cause of extinction. The data base is not adequate to choose between these hypotheses.

#### THE MIDDLE HOLOCENE DRY INTERVAL

The second environmental trend of interest is the early or middle Holocene interval that was drier and possibly warmer than today, the Altithermal of Antevs (1948). The case for such a climatic interval is strong at the eastern prairie/forest border, which had moved well east of its present position between about 8000 and 6000 yr B.P. (Webb et al., 1983). Using pollen/climate transfer functions, Bartlein et al. (1984) estimated that precipitation in the Minnesota area was about 20% less than it is today, but that temperature was only slightly higher. In the Great Plains, an extreme view of middle Holocene environmental change is that the entire Nebraska Sandhills was a vast area of desert dunes as a result of Altithermal drought (Ahlbrandt et al., 1983). This reconstruction is countered by direct evidence that the major dunes date to the late Pleistocene and not the Holocene (Wright et al., 1985).

Archeological evidence implies that the middle Holocene climate was dry enough in the heart of the Great Plains to reduce the density of the vegetation cover, which in turn diminished the bison herds as well as the human populations dependent on them (Frison, 1975, 1978). A tally of bison fossils in dated archeological sites in the southern plains shows a paucity of bison kill sites during the interval from 8000 to 4500 yr B.P. (Dillehay, 1974). Others, however, consider that the archeological evidence is inadequate to postulate significant reductions in human populations (Johnson and Holliday, 1986; Lynott, 1978; Reeves, 1973; Davis, 1987; Graham, 1987), and the issue remains unresolved (Stoltman and Baerreis, 1983).

Pollen studies carry information in addition to that implied by the transfer functions in the Midwest. For example, the middle Holocene dominance of herb pollen at sites in the present-day hardwood forest of west-central Minnesota, which is a record of the eastward retreat of the prairie/forest border, contains more *Artemisia* than presettlement samples from the eastern edge of the modern prairie (Jacobson and Grimm, 1986). *Artemisia* percentages this high (in comparison to *Ambrosia* and other herbs) are more characteristic of the mid-grass or short-grass prairie today than of the tall-grass prairie, which occupied western Minnesota at the time of settlement. The implication is that the prairie zones moved eastward during the middle Holocene, just as did the prairie/forest border. Near the western



edge of the tall-grass prairie, pollen diagrams from eastern South Dakota (Pickerel Lake: Watts and Bright, 1968; Medicine Lake: Radle, 1981) and northwestern Iowa (Lake West Okoboji: Van Zant, 1979) support this interpretation. In addition, studies in northwestern Minnesota suggest that the "prairie period" is more complex than originally thought. Sedimentologic and paleoecologic data from a varved lake record show at least two dry phases separated by a moister interval during the period from 8500 to 4000 yr B.P. (Dean et al., 1984). The macrofossil data from Kirchner Marsh in south-central Minnesota also imply major climatic fluctuations during the Altithermal (Watts and Winter, 1966).

The timing of the Holocene dry/warm interval appears to vary geographically. In Minnesota the maximum of Altithermal warmth and dryness occurred between about 8000 and 4000 yr B.P., peaking at 7200 yr B.P. (Wright, 1976). In the northwestern U.S. most sites register greatest drought in the early Holocene, about 10,500 to 7000 yr B.P. (Barnosky, 1984, 1985a, 1985b; Barnosky et al., in press; Mathewes, 1973; Alley, 1976; Davis et al., 1986; Beiswenger, 1984; Mack et al., 1978a; Mack, Rutter, and Valastro, 1978), although at some sites it was delayed until the middle Holocene, concurrent with the Midwest (Baker, 1976; Mehringer et al., 1977; Mack, Rutter, Valastro, and Bryant, 1978; Mack et al., 1978b, 1979, 1983; Nickmann, 1979). The differences in timing may be more apparent than real in the northwestern United States. Many of the sites featuring middle Holocene drought are missing the early Holocene record, presumably because the lakes dried or shallowed (Barnosky et al., in press).

The general tendency for an early Holocene warm/dry period in northwestern U.S. has been explained as a response to increased summer radiation between 12,000 and 9000 yr B.P. controlled by the Milankovitch earth/sun orbital variations (Barnosky et al., in press). Enhanced summer insolation amplified the subtropical high over the Northeast Pacific Ocean and thus intensified summer warmth and aridity across the Pacific Northwest and northern Rocky Mountains. In the early Holocene, the climate of the Midwest and northeastern United States was presumably still under the influence of the ice sheet and thus the Altithermal is expressed later, after the withdrawal of Laurentide ice well into Canada (Webb et al., 1983).

A few pollen records from the northern Great Plains provide clues to the Holocene climate in that region, but whether they are representative of the vast area is uncertain. A record from Swan Lake in the southwestern part of the Nebraska Sandhills indicates that an interdune depression contained a marsh from its inception about 9000 yr ago until about 3700 yr ago, when a lake developed because of a climatically controlled rise in water table (Wright et al., 1985). At Cottonwood Lake in central South Dakota, high percentages of Chenopodiaceae/Amaranthaceae pollen (Fig. 2), as well as degraded pollen, mark an interval of increased aridity, coinciding with lake drying in the middle Holocene. To the northwest, Guardipee Lake shows high ratios of *Artemisia* to Poaceae through the early Holocene (Fig. 3). Because pollen surface samples in the West indicate the general prevalence of *Artemisia* over Poaceae in drier regions (Mack and Bryant, 1974; McAndrews and Wright, 1969), the climate near Guardipee must have been more arid during the early Holocene than the late glacial or late Holocene. At Antelope Playa in northwestern Wyoming, the percentage data show trends similar to the Guardipee record, but Markgraf and Lennon (1986) reject these in favor of interpretations based on pollen accumulation rates and ostracods. Their conclusion of drier conditions after 5000 yr B.P. contradicts not only the



**GUARDIPEE LAKE**  
**Glacier County, Montana**  
**Analyst: C.W. Barnosky**

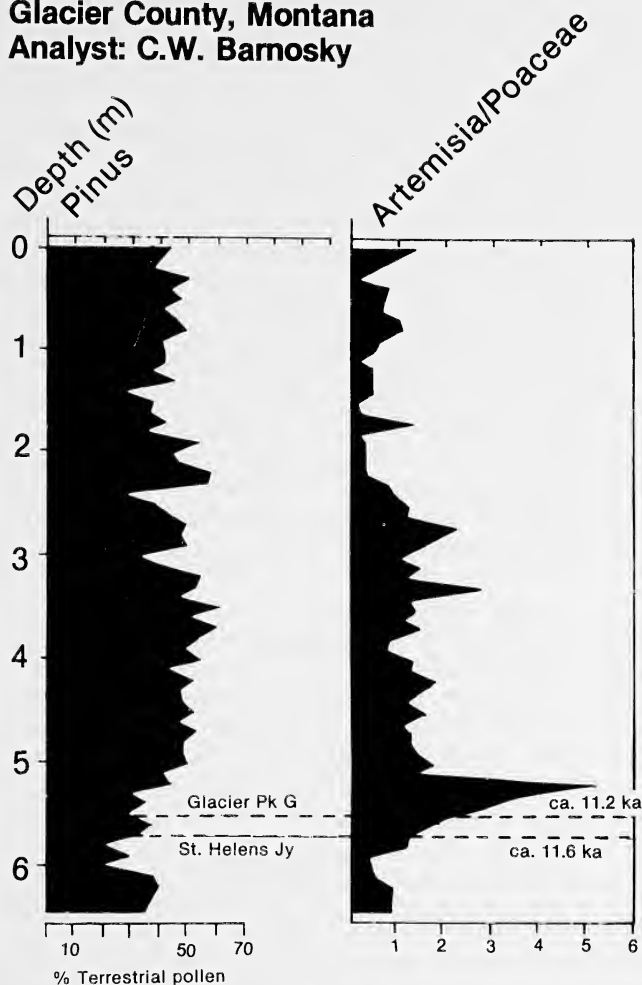


Fig. 3.—Pollen percentage curve for *Pinus* and the ratio of *Artemisia* to *Poaceae* pollen at Guardipee Lake, Montana. *Pinus* pollen is inferred to be from distant sources throughout the record. Dashed lines show the stratigraphic position of volcanic ash layers and their approximate age based on radiocarbon dates from other sites (Mehring et al., 1984; P. Carrara, personal communication, 1986). The *Artemisia*/*Poaceae* ratio is generally highest between 2.20 and 5.70 m and provides evidence of warmer and/or drier conditions in the early postglacial period. (ka = thousand years before present)

interpretation from Guardipee and other western pollen sites, but also evidence of conditions moister than present in the Laramie Basin of southeastern Wyoming, about 100 km to the south. From that area Wells (1970) reports late Holocene snags of *Juniperus scopulorum* and fossil woodrat middens with needles of juniper and ponderosa pine. The midden record includes 15 separately dated samples evenly covering the time range from about 200 to 2300 yr ago, with three additional dates to about 5600 yr ago. Because of the nature of the fossil occurrences, Wells (1970) is not able to detect a climatic trend within the late Holocene, only that conditions were probably wetter 200 to 5600 yr ago than they are at present.

Cooler/moister conditions in the late Holocene are also inferred from glacial advances during the Little Ice Age and Neoglaciation in the Rocky Mountains (Burke and Birkeland, 1983).

#### CONCLUSIONS AND IMPLICATIONS FOR FUTURE RESEARCH

There are several reasons why the postglacial history of the northern Great Plains is among the least well known in North America. First is the scarcity of natural lakes and wetlands suitable for paleoecologic study. Existing wetlands are often large shallow basins that contain mineral sediments with little organic matter and cannot easily be cored by the standard square-rod piston corer (Wright et al., 1983). The sites frequently yield an incomplete sedimentary record as a consequence of intermittent desiccation and deflation. Another problem is that in the glaciated areas of the northern Great Plains, the till contains carbonaceous shale, lignite, and limestone, all of which make standard radiocarbon dates of lake sediments unreliable. The more expensive accelerator method for dating plant remains must be used instead. Analysis of the pollen record poses additional problems that constrain the resolution of the vegetational reconstruction. The fossil grains from these sites are frequently degraded and difficult to identify. Furthermore, the common pollen types (for example, Gramineae, *Artemisia*, Chenopodiaceae/Amaranthaceae) include several species with great ecological amplitude.

Nonetheless, the available pollen studies with associated radiocarbon control permit a preliminary analysis of regional climate during glacial and postglacial time. At the glacial maximum the effect of the vast Laurentide ice sheet on the Great Plains climate was particularly great. The physical evidence for periglacial conditions in the northern Great Plains suggests a cold and windy climate. According to paleoclimatic model simulations, these winds were easterly or northeasterly because of the anticyclonic circulation over the ice sheet (Kutzbach and Guetter, 1986; Kutzbach and Wright, 1986). Their effect on full glacial vegetation to the south is not known in the absence of old sites, but in late glacial time, southerly winds generated by the diminished anticyclone are used to explain the rapid dispersal of *Picea glauca* into western interior Canada (Ritchie and MacDonald, 1986).

During the glacial maximum it is likely that open forest or parkland covered much of the northeastern Great Plains. The late glacial records seem to reflect the decline of periglacial conditions as the ice sheet thinned and retreated. By contrast, the western part was probably treeless in glacial time, with a low diversity of pollen types and low pollen accumulation rates, although this interpretation comes from records no older than 12,000 yr B.P. The opening of the Alberta corridor, although caused by increased temperature, may have brought colder, windier winter conditions to the south by letting previously trapped Arctic air escape from the polar region, but this effect was short-lived, as warming and ice retreat proceeded.

During the late glacial period summer insolation in the Northern Hemisphere was at a maximum, and seasonal contrasts were greatest. In the northern Great Plains, it seems likely that the western sector was dominantly under the influence of an insolation-forced climate, while the eastern sector experienced a periglacial climate. The vegetational expression of this boundary may be the western limit of the late Pleistocene spruce forest. Several eastern sites indicate late glacial sympatry of plants that are presently allopatric. The overlapping of taxa with

different tolerances of maximum and minimum temperatures implies reduced seasonality when the climate was under the influence of the ice sheet.

Today the Great Plains is the meeting place for Arctic, Caribbean, and Pacific air masses. Changes in their relative importance during the Holocene resulted in shifts in the location of major formational ecotones bordering the Great Plains grassland (Bryson, 1966; Bryson et al., 1970; Bartlein et al., 1984; Ritchie, 1976). Although the movement of formational ecotones peripheral to the northern Great Plains has been related to air mass regimes, this exercise has not been undertaken for the plains region itself. The Holocene climatic history in the northern Great Plains shows conditions that are intermediate between those in the Far West and Midwest. Just as in late glacial time, early Holocene warmth/aridity in the western part suggests a direct response to a climate driven by insolation changes. The eastern sites, on the other hand, imply a climate controlled by the retreating ice sheet until the middle Holocene. Model simulations show this contrast very nicely (Kutzbach and Guetter, 1986), but the interpretations from the few existing sites disagree. The South Dakota and North Dakota sites show middle Holocene aridity as predicted by the model. To the west, percentages of xerophytic taxa at Guardipee in northwestern Montana imply drought in the early Holocene, followed by greater effective moisture. Wood from southeastern Wyoming also suggests moist conditions in the late Holocene (Wells, 1970). But, at Antelope Playa in northeastern Wyoming, relatively moist conditions are inferred in the early Holocene from pollen accumulation rates and ostracod data (Markgraf and Lennon, 1986). The explanation for these apparent discrepancies lies in more well-dated sites.

The controversy surrounding the Pleistocene megafaunal extinction requires additional information about the past structure and composition of Great Plains vegetation. The environmental change hypothesis (Guthrie, 1984; Graham and Lundelius, 1984) states that during the Pleistocene the vegetation was structured as a mosaic rather than in the strongly zonal pattern of today. The documentation of parkland across much of the eastern plains would make this a compelling argument for the region as a whole (although it does not cause rejection of the overkill hypothesis). The environmental change hypothesis also assumes decreased seasonality during the Pleistocene, which can be tested by the late Pleistocene sympatry of plants now separated because of different seasonal tolerances.

Holocene vegetation and climate need better characterization to determine whether human and bison populations were reduced on the Great Plains during the Altithermal. Based primarily on the paucity of archeological sites in the middle Holocene, this hypothesis assumes that populations were low because extreme aridity limited food and water resources (Frison, 1975, 1978). Alternatively, persistent hunting by Indians may have kept bison populations below carrying capacity at all times (McDonald, 1984), in which case environmental changes had little if any impact on bison population size. Another possibility is that the paucity of middle Holocene archeological sites reflects the fact that these sites are deeply buried and not readily apparent at the surface (R. W. Graham, personal communication, 1987). Clearly further paleoecological and archeological as well as geomorphological research in this area is needed.

#### ACKNOWLEDGMENTS

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FOSSIL CRAB (DECAPODA: BRACHYURA) FAUNA FROM THE  
LATE CRETACEOUS (CAMPANIAN-MAASTRICHTIAN)  
PIERRE SHALE IN BOWMAN COUNTY, NORTH DAKOTAANNETTE B. TUCKER<sup>1</sup>RODNEY M. FELDMANN<sup>1</sup>F. D. HOLLAND, JR.<sup>2</sup>KENNETH F. BRINSTER<sup>3</sup>

## ABSTRACT

Twenty-seven specimens of brachyuran decapods from the Late Cretaceous Pierre Shale in Bowman County, North Dakota, have been referred to five species in five genera. Three specimens were assigned to *Ekalakia lamberti* Bishop, two to *Dakoticancer overanus* Rathbun, two to *Homolopsis punctata* Rathbun, 19 to *Raninella oaeensis* Bishop, and one to *Dioratiopus dawsonensis* (Bishop). These assignments extend the geographic ranges of all five genera into North Dakota and extend the stratigraphic ranges of *E. lamberti* and *D. dawsonensis*. The specimens were collected from three localities near the Little Missouri River in western Bowman County; all have been preserved as molds of the interior with only small fragments of integument.

## INTRODUCTION

Several specimens of decapod crustaceans were collected by one of us (KFB) during a study of molluscan paleontology of the Late Cretaceous Pierre Shale in Bowman County, North Dakota (Fig. 1). The decapod specimens were found in fossiliferous concretions collected as float from the upper 16 m of the Pierre. The dominant organic remains within the concretions consisted of gastropods, bivalves, scaphopods and cephalopods, with a relatively small number of decapod crustaceans. The mineralogy of the concretions is primarily calcite with some quartz and some clay minerals as determined by X-ray diffraction (Brinster, 1970).

The ages of these concretions were determined using baculitids within the various concretions. The *Baculites reesidei* and *B. grandis* biozones were recognized, while the intervening biozones of *B. jenseni*, *B. eliasi*, and *B. baculus* were not recognized by Brinster (1970).

Subsequently, W. A. Cobban (personal communication to FDH, 22 March 1979) identified one of Brinster's baculites (Loc. A1235) as *B. eliasi* and other ammonites (Loc. A1238) as *Didymoceras cheyennense* (Meek and Hayden) and *Oxybeloceras meekianum* (Whitfield) of late Campanian age. The apparent absence of intervening biozones may simply reflect the lack of recognition of them in Bowman County, to date. In the widely used ammonite zonation scheme for Late

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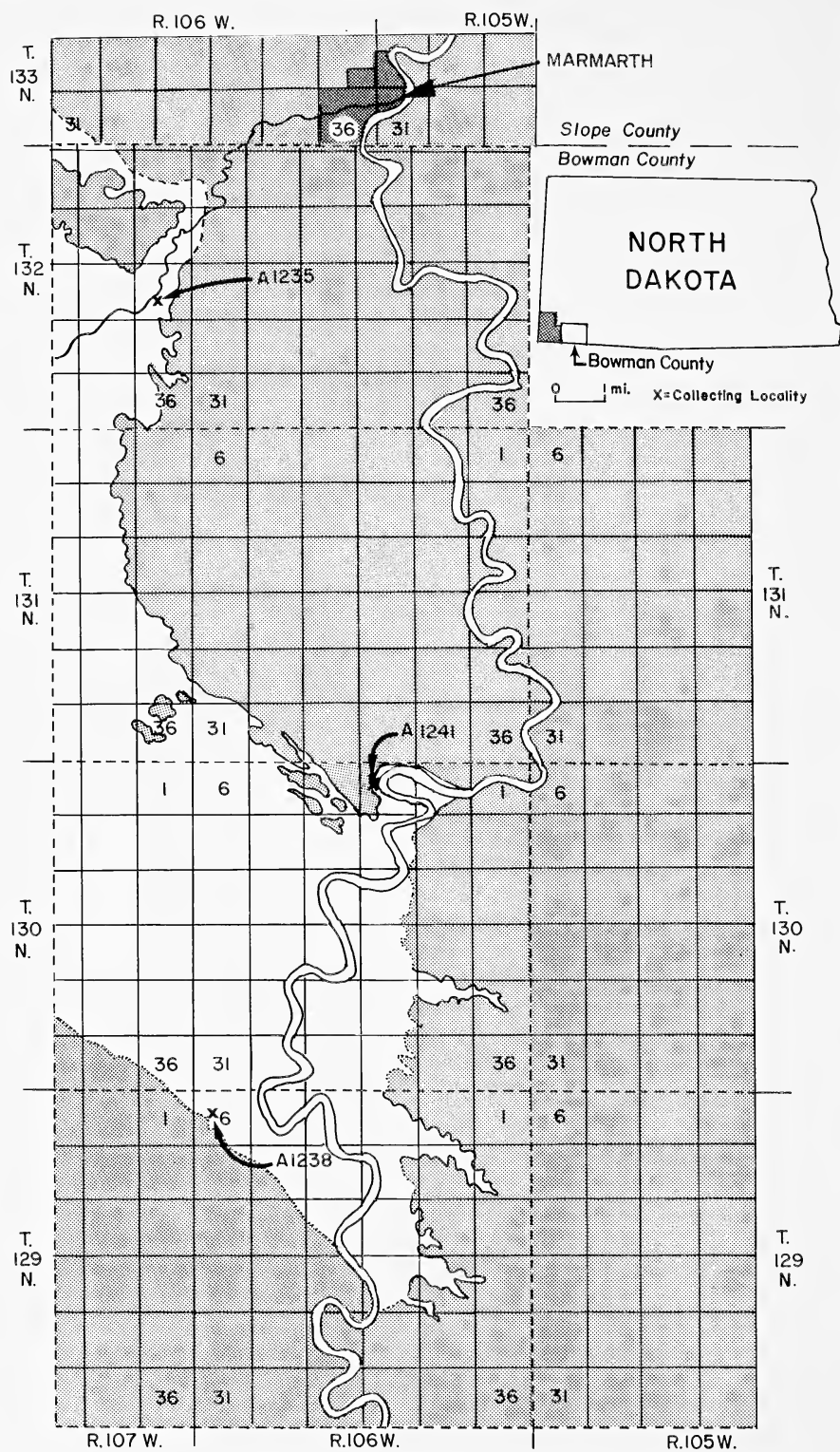


Fig. 1.—Map of contact between the Pierre Shale and the Fox Hills Formation showing localities in western Bowman County, North Dakota, from which fossil crabs were collected. Shaded area consists of Fox Hills and younger strata; dotted line indicates inferred contact. Geology by KFB.

Table 1.—Decapod faunas from the Pierre Shale and the Bearpaw Shale.

Reference	Geographic locality	Formation	Biozone	Age	Fauna
1	Dawson Co., Mont.	Pierre Shale	<i>Baculites baculus</i> , <i>B. grandis</i>	Maastrichtian	<i>Dioratiopus dawsonensis</i> (Bishop)
2	Carter Co., Mont.	Pierre Shale	unknown	Campanian or Maastrichtian?	<i>Ekalakia lamberti</i> Bishop
3	McCone Co., Mont.	Bearpaw Shale	<i>B. eliasi</i> or <i>B. jenseni</i>	Campanian, latest	<i>Hoploparia bearpawensis</i> Feldmann <i>Linuparus (Podocratus) pustulosus</i> Feldmann
4	Mobridge, S.D.	Pierre Shale	<i>B. grandis</i>	Maastrichtian	<i>Palaeonephrops browni</i> (Whitfield)
4	Corson, Dewey, Stanley, and Lyman counties, S.D.	Pierre Shale	<i>B. scotti</i> , <i>B. grandis</i>	Campanian, Maastrichtian	<i>Sodakus tatankayotankaensis</i> Bishop <i>Raninella oaheensis</i> Bishop
5	Creston, S.D.	Pierre Shale	<i>Didymoceras cheyennense</i>	Campanian	<i>Callianassa</i> sp., lobsters <i>Dakotacancer overanus</i> Rathbun <i>Homolopsis punctata</i> Rathbun <i>Necrocarcinus pierrensis</i> Rathbun <i>Callianassa</i> sp., <i>D. overanus</i> , <i>H. punctata</i> , <i>N. pierrensis</i> , lobsters
5	Thompson Butte, S.D.	Pierre Shale	<i>D. stevensoni</i> <i>D. nebrascense</i> <i>Exiteloceras jenneyi</i> <i>Baculites rugosus</i> ?	Campanian	
5	Mobridge and Promise, S.D.	Pierre Shale	<i>B. grandis</i>	Maastrichtian	<i>Callianassa</i> sp., <i>D. overanus</i> , <i>H. punctata</i> , <i>Sodakus tatankayotankaensis</i> Bishop, <i>N. pierrensis</i> , <i>R. oaheensis</i> , lobsters

Table 1.—Continued.

Refer- ence	Geographic locality	Formation	Biozone	Age	Fauna
6	Mobridge Locality, S.D.	Pierre Shale	<i>B. grandis</i>	Maastrichtian, early	<i>Zygastrocarcinus mendryki</i> (Bishop)
7	Valley Co., Mont., Bitter Creek Lo- cality			Campanian, late	<i>Zygastrocarcinus griesi</i> Bishop <i>Notopocorystes (Eucorystes) eichhorni</i> Bishop
8	Larimer, Colo.	Pierre Formation	<i>B. reesidei</i> , <i>B. jenseni</i>	Campanian, latest or Maastrichtian, earli- est	<i>Eomunidopsis cobbani</i> Bishop
9	Black Hills, S.D.	Gammon Ferrugi- nous Member, Pierre Shale	<i>B. baculus</i> , <i>Baculites</i> sp. (smooth)	Campanian, latest or Maastrichtian, earli- est	<i>Protocallianassa russelli</i> Bishop, <i>Nec- rocarcinus davisi</i> Bishop, <i>Hoplo- paria nickelsoni</i> Bishop <i>Rugafarius fredrichi</i> Bishop <i>Dioratiopus hearttailensis</i> Bishop <i>Xanthosia elegans occidentalis</i> , <i>Rani- nella oahensis</i>
10	Bowman Co., N.D.	Pierre Shale	<i>B. reesidei</i> , to <i>B. grandis</i>	Campanian, late to Maastrichtian, early	<i>Ekalakia lamberti</i> <i>Dakotacancer overanus</i> <i>Homolopsis punctata</i> <i>Raninella oahensis</i>
11	Butte Co., S.D.	Pierre Shale	<i>Baculites</i> sp. (smooth)	Campanian, mid-early	<i>Dioratiopus dawsonensis</i> <i>Dromiopsis kimberlyae</i> Bishop

References: 1) Bishop, 1973; 2) Bishop, 1976; 3) Feldmann, Bishop, and Kammer, 1977; 4) Bishop, 1978; 5) Bishop, 1981; 6) Bishop, 1982; 7) Bishop, 1983; 8) Bishop, 1985a; 9) Bishop, 1985b; 10) this study; 11) Bishop, 1987.

Cretaceous strata of the Western Interior (Gill and Cobban, 1966:A28-A35; Gill and Cobban, 1973:4; Kennedy and Cobban, 1978:70; Scott and Cobban, 1986), the exposed part of the Pierre Shale in Bowman County, therefore, ranges from late Campanian to early Maastrichtian age.

The Pierre Shale extends over a broad area of the Western Interior of North America. Most exposures are located in north-central Montana and in central South Dakota. Outcrops of the Pierre also occur in the Black Hills in South Dakota and Wyoming, along the flanks of other uplifts in the Rocky Mountain region, and in south-central and extreme southwestern North Dakota. Much of the Pierre Shale is concealed by younger rocks or by glacial debris (Tourtelot, 1962). Lateral equivalents of the Pierre Shale include the Claggett Shale, the Judith River Formation, and the Bearpaw Shale in Montana. The Pierre is conformably overlain by the Fox Hills Formation with a gradational change from a fine, silty, clay shale of the upper Pierre Shale to a sand, silty clay or shaly silt of the lower Fox Hills Formation (Waage, 1961).

Exposures of the Pierre Shale in Bowman County result from erosion of the eastern flank of the Cedar Creek anticline (Fig. 1). The axis of the asymmetrical anticline is oriented northwest-southeast; beds dip steeply on its southwest flank and gently on its northeast flank (Bishop, 1965). The Little Missouri River cuts the southeastern tip of the structure. Little Beaver Creek which empties into the Little Missouri River cuts the anticline normal to its axis.

The purpose of this paper is to describe the decapods from Bowman County, North Dakota, and to compare them to those described by Bishop and others from South Dakota, Montana, and Colorado (Table 1). Descriptive treatment of the different taxa varies in length and detail depending upon the need to augment previous descriptions. Extensions in the geographic and stratigraphic ranges of the decapod taxa are noted, as well.

The decapod specimens were found in concretions from the three localities given below. Measured specimens, their catalog numbers in The Carnegie Museum of Natural History paleontological collection, and their University of North Dakota accession numbers are listed in Table 2. The localities are:

- A1235      Float below east bank of Little Beaver Creek, NE¼ SW¼ sec. 24, T132N, R107W, Webster NE Quadrangle, Montana-North Dakota, Bowman County, about 6 miles southwest of Marmarth, Slope County, North Dakota (KFB field no. 69-9c).
- A1238      Float in creek bottom, SE¼ NW¼ sec. 6, T129N, R106W, Cedar Ridge Quadrangle, Bowman County, about 20 miles south of Marmarth, Slope County, North Dakota (KFB field no. 69-12).
- A1241      Float below west bank of Little Missouri River, SE¼ NW¼ sec. 3, T130N, R106W, Cedar Ridge Quadrangle, Bowman County, about 12 miles south of Marmarth, Slope County, North Dakota (KFB field no. 69-17).

#### SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1803  
 Suborder Pleocyemata Burkenroad, 1963  
 Infraorder Brachyura Latreille, 1803  
 Section Podotremata Guinot, 1977  
 Subsection Dromioidea Guinot, 1977  
 Superfamily Dromioidea de Haan, 1833  
 Family Prosopidae von Meyer, 1860

Subfamily Prosopinae von Meyer, 1860  
Genus *Ekalakia* Bishop, 1976

*Type species.*—*Ekalakia lamberti* Bishop, 1976.

*Ekalakia lamberti* Bishop, 1976  
Fig. 2.1–2.3

*Preservation.*—Three specimens can be referred to *Ekalakia lamberti* Bishop. The largest is a well-preserved, complete mold of the interior; pitting, caused by dissolution of the calcitic mud filling, occurs over the entire specimen. A smaller specimen is a well-preserved, complete mold of the interior with the anterior portion of the rostrum absent. The thoracic region of the smaller, complete specimen exhibits slight exfoliation. A third specimen is a poorly preserved mold of the interior with the anterior one-third fractured and somewhat displaced. The appendages, abdomen, and sternum are not preserved on any of the specimens.

*Remarks.*—The specimens agree in most respects with *Ekalakia lamberti* Bishop. The carapace is longer than wide, strongly convex transversely, and convex longitudinally. The rostrum is downturned and has a median sulcus which splits into fainter grooves posteriorly on both sides of the mesogastric and metagastric regions. There is a U-shaped, subparallel depression between the protogastric and epigastric regions. There are also cervical and branchiocardiac furrows which are U-shaped, subparallel and equally deep. The metabranchial regions are inflated and the cardiac region is raised well above the rest of the carapace.

The specimens differ from the original description of *E. lamberti* in that a node is situated on the posterior cardiac region of the largest specimen (Fig. 2.2). In addition, two well-developed tubercles occur on the mesogastric region and one tubercle is developed on the metagastric region of the two complete specimens. The occurrence of this node and the tubercles, however, does not warrant naming a new species. The branchial region is pustulose and the branchial region of the largest specimen is more inflated than that of the smaller, complete specimen making the larger specimen appear to be more vaulted (Fig. 2.2–2.3). The posterior portion of the broken specimen is well preserved and the morphology of this, together with various length-width ratios similar to those of the other two specimens, strongly suggests that it belongs in *E. lamberti* (Fig. 2.1). Although the inflated branchial region, as well as the rapidly narrowing anterolateral margin,

Table 2.—Decapod Fauna, Pierre Shale, Bowman County, North Dakota. An additional sixteen specimens of *Raninella oaheensis* are from UND locality number A1238.

Species	Carnegie Museum Paleontology Catalog No.	UND loc. no.	Length	Width
<i>Ekalakia lamberti</i>	CM 34558	A1238	13.6 mm	12.2 mm
	CM 34559	A1235	8.8 mm	7.8 mm
	CM 34560	A1238	10.0 mm	8.3 mm
<i>Dakoticancer overanus</i>	CM 34561	A1241	14.4 mm	15.4 mm
	CM 34562	A1235	16.7 mm	broken
<i>Homolopsis punctata</i>	CM 34563	A1241	10.0 mm	8.0 mm
	CM 34564	A1241	6.7 mm	5.0 mm
<i>Raninella oaheensis</i>	CM 34565	A1238	17.9 mm	10.2 mm
	CM 34566	A1238	16.0 mm	9.8 mm
	CM 34567	A1238	16.2 mm	10.1 mm
<i>Dioratiopus dawsonensis</i>	CM 34582	A1238	16.2 mm	14.8 mm



Fig. 2.—*Ekalakia lamberti* Bishop; dorsal view of carapaces. 1, CM34560. 2, CM34558. 3, CM34559. Scale bars equal 1 cm.

causes this specimen to resemble the majids; conservatively, it should be referred to *E. lamberti*.

Superfamily Dakoticancroidea Rathbun, 1917

Family Dakoticancridae Rathbun, 1917

Genus *Dakoticancer* Rathbun, 1917

*Type species.*—*Dakoticancer overanus* Rathbun, 1917.

*Dakoticancer overanus* Rathbun, 1917

Fig. 3.1, 3.2

**Preservation.**—Two specimens have been identified as *Dakoticancer overanus* Rathbun. The larger specimen is a partially broken mold of the interior; the right side is complete while the left side is incomplete. The smaller specimen is a complete, very well-preserved mold of the interior with some adherent, exfoliating integument.

**Emendation to description.**—Carapace thick, deeply grooved, and slightly wider than long. Dorsal surface convex longitudinally, front severely downturned anterior to the cervical groove; slightly convex transversely. Surface of carapace finely granulate on raised portions; intermediate areas smooth to finely punctate.

Width of fronto-orbital region approximately one-half greatest width. Orbits circular in outline; margins flare outward and upward; outer orbital margin bears one dorsal and one ventral tooth. Proximal portion of rostrum sulcate with raised rims; length undetermined; downturned.

Anterolateral margin convex in outline with a nearly vertical sidewall. Margins below hepatic region marked by well-defined rim and shallow furrow which extends backward and upward to form groove separating mesobranchial and metabranchial regions. Posterolateral margin weakly sigmoid. Posterior margin slightly convex with marginal rim and furrow.

Epigastric regions on either side of posterior rostral sulcus broadly swollen centrally; regions poorly defined by broad shallow grooves. Interior groove of epigastric region is posteriad continuation of rostral sulcus; grooves separating epigastric from protogastric regions converge posteriorly from frontal margin. Protogastric regions defined by shallow grooves; two interior shallow longitudinal furrows diverge posteriorly from rostral sulcus to separate protogastric and mesogastric regions; shallow furrows, parallel to diverging interior furrows, separate protogastric and hepatic regions. Hepatic regions swollen and pustulose. Transverse, deeply-etched cervical groove defines posterior margins of hepatic and protogastric regions; a deep pit marks juncture of posterior protogastric-hepatic furrow and cervical furrow. Protogastric regions swollen posteriorly. Transverse cervical groove not crossing mesogastric-cardiac region. Longitudinal furrows converge gradually until they almost meet at posterior margin of carapace; furrows interrupted by shallow pits on either side of anterior intestinal region. Another transverse groove separates mesobranchial and metabranchial regions; groove interrupted at midpoint so that incision is incomplete between cardiac and intestinal regions. Mesobranchial region bears inflated boss at midpoint; boss tapers into ridge which extends forward and down along side-wall.

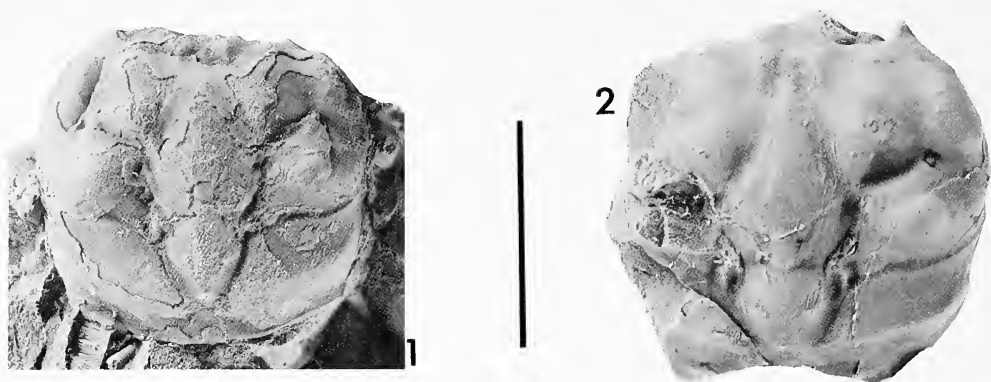


Fig. 3.—*Dakoticancer overanus* Rathbun; dorsal view of carapaces. 1, CM34561. 2, CM34562. Scale bars equal 1 cm.

Metabranial region with central ridge which extends gently forward to lateral margin where it abruptly terminates. Cardiac region gently swollen and marked centrally by two arcuate depressions on either side of midline; anterior portion of depressions marked by pits.

A series of nodes ornaments dorsal carapace. One small node occurs just above each orbit; series of three nodes forms an inverted triangle on posterior-most portion of intestinal surface.

*Remarks.*—These specimens conform, in most respects, to the description of *Dakoticancer overanus* Rathbun. The carapace is thick and deeply grooved; the front, between the eyes, is small; the orbits are well defined; the carapace is covered with small granules.

The specimens differ from the description by Rathbun of *D. overanus* in that the mesobranial regions bear inflated bosses (Fig. 3.1–3.2). Several of Bishop's (1981) illustrations of *D. overanus* also clearly show bosses on the mesobranial regions of those specimens. However, the recognition of these bosses does not warrant the naming of a new species. The original description of the mesobranial regions of *D. overanus* was unclear.

Superfamily Homoloidea White, 1847

Family Homolidae White, 1847

Genus *Homolopsis* Bell, 1863

*Type species.*—*Homolopsis edwardsii* Bell, 1863.

*Homolopsis punctata* Rathbun, 1917

Figs. 4.1–4.3, 5

*Remarks.*—Two specimens of *Homolopsis punctata* Rathbun have been identified. The larger specimen is a well-preserved, partially exfoliated mold of the interior of a carapace broken longitudinally along the *linea homolica*; the rostrum is absent (Fig. 4.2).

The smaller specimen is a very well-preserved juvenile that is also a mold of the interior of a carapace broken along the *linea homolica* (Fig. 4.3). The rostrum, separated from the carapace, is preserved as a mold of the exterior.

The specimens agree in most respects with *Homolopsis punctata* Rathbun. The anterior one-third of the carapace curves strongly downward. The imprint of the rostrum of the smaller specimen confirms that the rostrum is sharply downturned. The elevations form regularly placed bosses: one boss on each epigastric lobe,





Fig. 4.—*Homolopsis punctata* Rathbun; dorsal view of carapaces. 1, Holotype USNM32058. 2, CM34563. 3, CM34564. Scale bars 1 & 2 equal 1 cm; scale bar 3 equals 1 mm.

three larger bosses and one small boss on each protogastric lobe, one anterior node and a posterior boss on the mesogastric region, two kidney-shaped nodes on the metagastric region, and one small boss and two large bosses on each epibranchial lobe. The cardiac region is urn-shaped and is broadly swollen into a dome in the posterior portion; the domed region is not nodose. Deep grooves delineate the hepatic, gastric, mesobranchial, and cardiac regions. The surface of the carapace is finely punctate. The posterior margin is bordered by a thin raised rim.

These characters strongly resemble those of *Homolopsis dispar* Roberts (1962) from the Late Cretaceous Merchantville Formation in New Jersey. In addition, there is a pronounced similarity in the preserved right lateral margins of the holotype of *H. punctata* (Fig. 4.1) and *H. dispar* (Fig. 5); each specimen bears a well-preserved epibranchial lateral spine which is aligned in a similar manner with an epibranchial boss just within the *linea homolica*. These similarities confirm the synonymy proposed by Wright and Collins (1972:46) of *H. dispar* with *H. punctata*. The absence of the anterior mesogastric node on *H. dispar* and the dissimilarities in the size of some of the nodes when compared to *H. punctata* serve to illustrate the variation among individuals within this species. In fact, the



Fig. 5.—*Homolopsis punctata* Rathbun (= *H. dispar* Roberts). Dorsal view of carapace of the holotype of *H. dispar*, ANSP20030. Scale bar equals 1 cm.

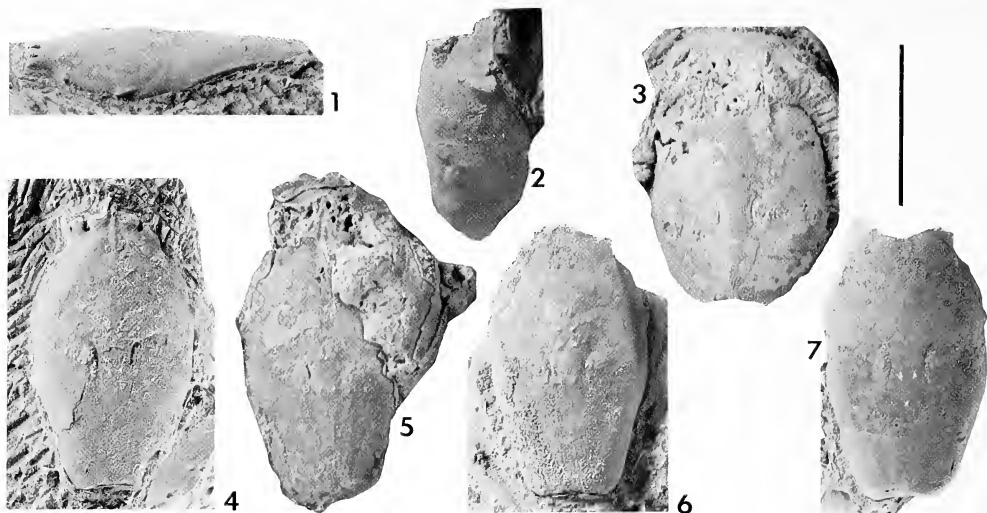


Fig. 6.—*Raninella oaheensis* Bishop. 1, Left lateral view of carapace, CM34565. 2, Oblique anterior view showing right orbital ventral fissures, CM34566. 3, Dorsal view of carapace, paratype USNM 173581, exhibiting bite marks. 4, Dorsal view of carapace, CM34565. 5, Dorsal view of carapace, holotype USNM 173589. 6, Dorsal view of carapace, CM34567. 7, Dorsal view of carapace, CM34566. Scale bar equals 1 cm.

range of variation between specimens from the Pierre Formation is as great, or greater, than that between the New Jersey material and the specimens from the Pierre.

Subsection Archaeobrachyura Guinot, 1977  
 Superfamily Raninoidea de Haan, 1833  
 Family Raninidae de Haan, 1833  
 Subfamily Ranininae Serene and Umali, 1972  
 Genus *Raninella* A. Milne Edwards, 1862

*Type species.*—*Raninella trigeri* A. Milne Edwards, 1862.

*Raninella oaheensis* Bishop, 1978

Fig. 6.1–6.7

*Preservation.*—Nineteen specimens have been referred to *Raninella oaheensis* Bishop. Most of the specimens are broken; however, three specimens used for description are nearly complete molds of the interior. One specimen exhibits a well-preserved frontal region; another is a mold of the interior, with adhering portions of the integument that illustrate the distribution of the dorsal nodes. A third specimen has preserved the ventral orbital fissure.

*Emendation to description.*—Carapace ovate in outline, widest in anterior one-third, greatest width about 60% of total length. Surface finely punctate. Carapace slightly convex longitudinally and very convex transversely. Lateral margins turned under carapace (Fig. 6.1).

Width of fronto-orbital region 63% of greatest width. Fronto-orbital region widest anteriorly, tapering posteriorly; orbits directed slightly away from long axis, ovate, height approximately one-half width; margins of orbits thicken and flare outward and upward. Dorsal margin of each orbit marked by two deeply grooved, open fissures, each about twice as deep as wide that approximately parallel lateral margins of orbits; axes of fissures converge posteriorly toward midline of carapace; median fissures about twice as deep and twice as wide as lateral fissures (Fig. 6.4). Each ventral orbital margin with one open fissure near lateral margin (Fig. 6.2). Frontal margin of carapace produced to form rostrum

that extends well beyond orbits, not downturned. Rostrum long, triangular in outline with straight margins, keeled medially; keel subtle, extending onto carapace a distance greater than length of rostrum; keel bounded laterally by shallow sulci (Fig. 6.4–6.5).

Anterolateral margin of carapace convex in outline, bearing two pairs of short spines; pair of hepatic spines point outward and slightly forward, pair of lateral spines point forward and slightly outward. Posterior lateral spines define greatest width of carapace. Posterolateral margin weakly sigmoid, with carapace tapering to narrow, blunted, posterior margin; posterolateral margin with narrow, well-defined, marginal rim and furrow; margin turned under carapace. Posterior margin smoothly concave with marginal rim and furrow.

Midline of carapace slightly keeled from rostrum to posterior mesogastric region where keel merges into cardiac region; cardiac region gently and broadly swollen, flattening to posterior margin. Urn-shaped cardiac region defined by pair of shallow grooves; anterior two-fifths deeply etched as arcuate impressions curving toward midline from a position at midlength of carapace, becoming less prominent posteriorly; remainder of groove subtle (Fig. 6.3–6.7).

Cardiac region with four nodes; a pair of nodes on either side of midline on a transverse line passing through posterior end of deeply impressed portion of cardiac grooves and another pair on either side of midline on transverse line just anterior of cardiac grooves. A pair of gastric pits occurs on either side of midline on transverse line between lateral spines; gastric pits with raised medial margins form nodes and begin series of small nodes forming curved lines that extend forward and diverge from midline axis. Just anterior to gastric nodes, three nodes form a triangle with its base on transverse line between lateral spines and its apex directed anteriorad. Two larger gastric nodes occur anteriorad apex of nodal triplet. All nodes most obvious where carapace has been exfoliated; subtle on surface of integument. No other grooves present. Hepatic region bears pustulose prosopon (Fig. 6.1).

*Remarks.*—*Raninella trigeri* A. Milne Edwards, type species of the genus, has both pairs of marginal spines pointing forward; the spines are much more robust than in *R. oaheensis*. The posterolateral margin is convex in *R. trigeri* and not sigmoid as in *R. oaheensis*. *Raninella eocenica* Rathbun (1935) is widest a little behind the midpoint and possesses a long, cylindrical spine on the outer margin of each orbit. *R. oaheensis* has a longer, more narrow rostrum, not downturned, than that in *Raninella tridens* Roberts (1962); the rostrum of *R. oaheensis* is keeled medially, not excavated as in *R. tridens*. The orbits of *R. tridens* have closed fissures on both upper and lower margins. *Raninella mucronata* Rathbun (1935) is widest at the midpoint and the posterolateral margins converge rapidly posterior of the midpoint. *Raninella carlilensis* Feldmann and Maxey (1980) has nearly circular orbits with closed fissures on the rims; the rostrum is shorter than in *R. oaheensis*; the deeply impressed gastric grooves observed in *R. oaheensis* are fainter in *R. carlilensis*.

Superfamily Tymoloidea Alcock, 1896  
Family Torynommidae Glaessner, 1980  
Genus *Dioratiopus* Woods, 1953

*Type species.*—*Dioratiopus salebrosus* Woods, 1953.

*Dioratiopus dawsonensis* (Bishop) 1973

*Preservation.*—This species is represented by one complete, very well-preserved, exfoliated mold of the interior. The distal portion of the rostrum is absent, and the proximal portion of the rostrum has been cracked transversely and is displaced slightly. The appendages, abdomen, and sternum are not preserved.

*Emendations to description.*—Frontal region with slightly downturned, sulcate rostrum with raised proximal rims and one proximal spine (Fig. 7). Another spine on dorsal, interior rim of orbit. Outer extension of orbit marked by forwardly directed hepatic spine. Protogastric region divided posteriorly by shallow, longitudinal furrow parallel to groove between mesogastric and protogastric regions into a swollen adaxial area and an outer area bearing two nodes.

*Remarks.*—Glaessner (1980:182) considered *Glaessnerella* Wright and Collins,



Fig. 7.—*Dioratiopus dawsonensis* (Bishop). Dorsal view of carapace, CM34582. Scale bar equals 1 cm.

1975 (= *Glaessneria* Wright and Collins, 1972) to be the junior, subjective synonym of *Dioratiopus*. Although considered closely allied by Wright and Collins (1972:33), *Glaessnerella* was distinguished from *Dioratiopus* by being much less vaulted in both transverse and longitudinal section. *Glaessnerella* also lacks an inner, oblique sulcus on the mesobranchial area and has a more strongly spinose frontal area than *Dioratiopus* (Wright and Collins, 1972). However, Glaessner (1980) did not consider these differences to be reliable generic characters. He assigned *Dioratiopus* Woods to his new family, Tornyommidae in the Tymoidea. He considered the Tornyommidae to be a natural taxon since it separates the Cretaceous genera of widely-distributed, shallow-water crabs from some of their deep-water descendants. Glaessner (1980) also reassigned *Homolopsis dawsonensis* Bishop to *Dioratiopus* because of the absence of a *linea homolica* and the presence of weaker ornamentation than that found on *Homolopsis*. Bishop (1985b: 616) concurred with this reassignment.

*Discussion.*—The specimen exhibits the following family characters: the carapace is pentagonal but only slightly longer than wide; it is convex transversely and slightly convex longitudinally; the front is spatulate, projecting, and not sharp; the sidewalls are steep; the orbits are shallow. The remainder of the family characters are not preserved on this specimen.

The specimen agrees with the generic characters of *Dioratiopus* Woods, 1953. The carapace is pentagonal and longer than broad. The cervical and branchial grooves are equally well-developed and the sidewalls are nearly vertical. The rostrum is produced to form a short, anteriorly directed triangle. The orbits are shallow and form wide depressions.

The specimen conforms in every respect to the original description of this species (Bishop, 1973). With the preserved frontal region including the rostral area, the shape of the carapace is pentagonal.

#### CONCLUSIONS

This study represents the first examination of brachyurans from the upper Pierre Shale in Bowman County, North Dakota and, as such, expands the geographic

range of the five genera represented. *Ekalakia lamberti* Bishop, 1976 has had no previously definitive biostratigraphic association. As a result of the association with *Baculites reesidei* and *B. grandis*, a range of late Campanian to early Maastrichtian is confirmed for this species.

The material of this study represents an assemblage dominated by *Raninella oaheensis* Bishop, 1978. Bishop has suggested a Campanian-Maastrichtian range for this species that is confirmed by this study, as is the Campanian-Maastrichtian range of *Homolopsis punctata* and *Dakoticancer overanus*. *Dioratiopus dawsonensis* (Bishop) was originally reported from the zones of *Baculites baculus* and *B. grandis* suggesting a Maastrichtian age for this species (Bishop, 1973:19). Although Bishop (1985b:618) extended the North American range of the genus back into the Campanian with the description of *D. hearttailensis*, this study suggests that the range of *D. dawsonensis* also be extended to include late Campanian.

#### ACKNOWLEDGMENTS

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EXCAVATIONS AT THE HARNEY SITE SLAVE CEMETERY,  
MONTSERRAT, WEST INDIES

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## ABSTRACT

An archaeological salvage project at the Harney site, Montserrat, recovered parts of ten human skeletons from burials exposed in trenches dug by construction workers during excavation of a house foundation. Osteological analysis of these skeletons and additional bones previously removed by construction workers identified 17 individuals. Several burial patterns were discernible despite the disturbed nature of the Harney site and incomplete condition of its skeletons. The patterns include placement of bodies in graves dug to a rock stratum underlying the site, interment in a west-headed direction, and arrangement of the corpses on their backs with legs extended. The presence of nails in some graves provides suggestive but not conclusive evidence for the use of coffins or some other form of burial apparatus. Recovered artifacts indicate this unmarked and unrecorded cemetery was used at least in the latter eighteenth century and possibly longer. The most unusual artifact was an intact Turlington Balsam of Life phial dated OCT 29 1751.

## INTRODUCTION

When human skeletons were exposed by a construction crew digging a house foundation near Bransby Point, the Montserrat National Trust asked the author, who was on the island conducting prehistoric archaeological research, to examine the remains. It soon became evident the construction crew had encountered an unmarked and unrecorded cemetery site, a finding that led to a six-day salvage excavation project between 29 June and 4 July 1979.

The burial ground was named the Harney site (MS-A-H4) in recognition of St. Clair Harney, the contractor who permitted the salvage project to take place despite the disruption it caused in the construction schedule. Bones were first uncovered by the construction crew about ten days before the author was scheduled to leave Montserrat, after having completed his dissertation field research on prehistoric sites (Watters, 1980).

This article treats the burial excavations and artifacts found at the Harney site salvage project. A second article (Mann et al., 1987) deals with the detailed osteological analyses of the skeletons.

## SITE DESCRIPTION

Montserrat, with an area of 102 km<sup>2</sup> (39.5 mi<sup>2</sup>), is one of the smaller islands of the northern Lesser Antilles (Leeward Islands) in the eastern Caribbean Sea. It is located on the inner or volcanic arc of the Lesser Antilles. Three major volcanic centers trending north to south, Silver Hill, Centre Hills, and Soufrière Hills, dominate the island's landscape (Fig. 1). West of Centre Hills near the leeward coast are two smaller volcanic centers, St. George's Hill and Garibaldi Hill. Watters (1980:103-136) and Steadman et al. (1984) provide additional information about Montserrat's physiography.

The triangular rocky headland of Bransby Point, the westernmost point of land

Submitted 5 May 1987.

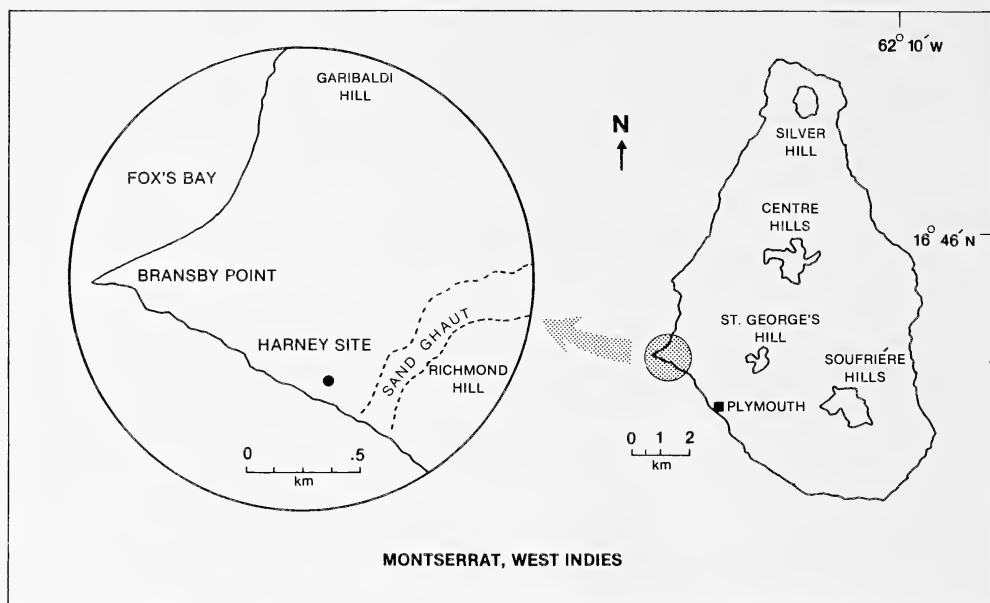


Fig. 1.—Location of the Harney site in relation to Bransby Point on the west coast of Montserrat.

on Montserrat, is about 1.8 km NW of Plymouth, capital of the island (Fig. 1). Bransby Point is formed by a horizontal bed of coarse but well-consolidated agglomerate overlaying fine-grained tuff (MacGregor, 1939:39). Martin-Kaye (1959: fig. 12) labels the latter material "Bransby tuff." A valley begins north of Bransby Point at Fox's Bay and trends east to the base of St. George's Hill. The valley is flanked by Garibaldi Hill on the north and the much lower Richmond Hill on the south. Along the southern border of the valley, a ridge runs SSW to the leeward coast.

The Harney site is located on the lower slope of that ridge (UTM coordinates NP818484) near the 90-ft contour line. The site is separated from Richmond Hill by Sandy Ghaut, a generally dry watercourse (Fig. 1), and it lies some 50 m inland from the coastal cliff reaching a height of about 15 m above a narrow cobble beach.

Construction work had disturbed the Harney site before the author was apprised that bones had been found. Later interviews with the contractor established that as much as two meters of soil had been removed from parts of the site by bulldozers while leveling the landscape. Conspicuous and numerous backdirt piles attested to the amount of overburden removed. It was while the construction crew, using picks and shovels, was digging footers across the site that the skeletal materials were first revealed.

Fragmented bones found in these trenches were initially regarded by the construction crew as being "old cattle bones." However, the foreman, Jackie Dangler, who had been a military medic, thought the bones were human. The workers concurred with Dangler's evaluation after a jaw, undoubtedly human, was recovered from one trench. Dangler put the bones in a paper sack and buried it in an isolated part of the site, away from the main digging area. Several days later, the author was notified of the finds and went to the site to investigate the remains.



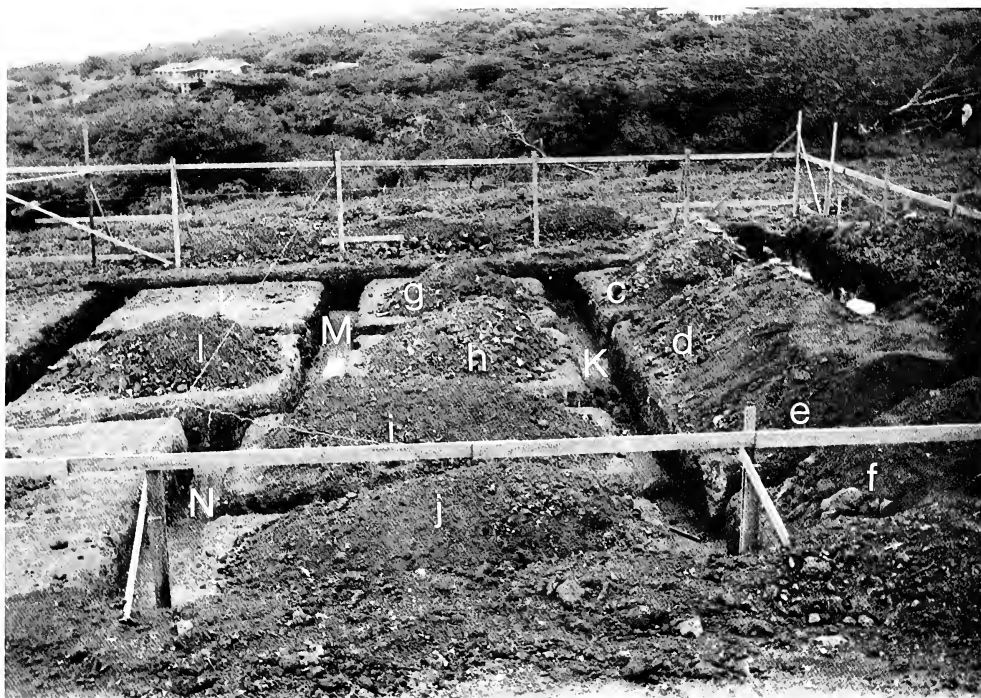


Fig. 2.—View looking NW of the grid pattern of platforms (lower case letters) and trenches (upper case) excavated by the construction workers (see Fig. 3).

#### METHODOLOGY

By the time the author arrived, the workers already had dug many footers and produced a grid pattern of trenches bordering a series of raised platforms (Fig. 2). The tops of these platforms were artificial surfaces (not the original land surface) created when the overburden was removed by bulldozers. Soil dug from the trenches had been piled atop the platforms. Beyond the wood frame outlining the building site were the backdirt piles left by the bulldozers.

Dangler indicated the areas in the footers where bones had been exposed beforehand. Fragmented bones protruding from the sides of various platforms indicated that pick and shovel activity already had damaged some skeletons. Footers had been dug through the soil layer into a rock stratum underlying the site.

Dangler also pointed out the location of the buried paper sack. When dug up, it was found to contain many broken bones. The construction workers confirmed that the breaks, clearly recent in origin, resulted from their pick and shovel activity. These bones, which had been found in widely separated areas of the site, came from more than one individual and, therefore, were termed the "multiple burial." The sack also yielded historic artifacts (a glass phial, three clay pipe stems, one pipe bowl, and seven rusted nail fragments). These artifacts confirmed the skeletons to be historic rather than prehistoric burials.

The author was examining the items in the sack when the construction crew, working in a trench in another part of the site, uncovered yet another burial. By that time, it was evident the house foundation was being dug in a cemetery site.

It was decided that an archeological salvage project was the logical strategy to

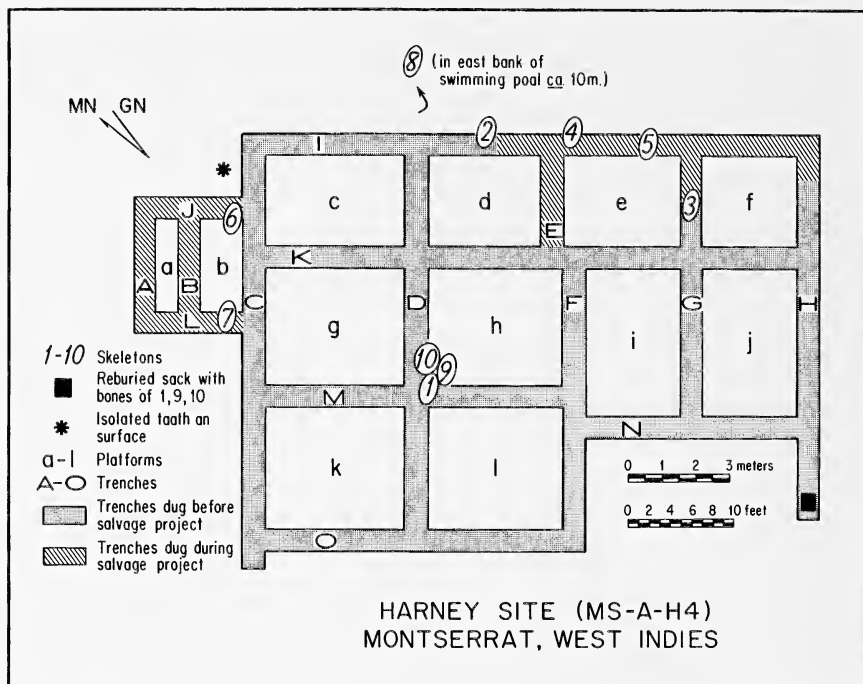


Fig. 3.—Planview of the Harney site showing locations of the *in situ* skeletons in relation to the grid.

adopt at the Harney site, given the previous disturbance, limited time for excavation, and few personnel available. For six days, the author and four volunteers, Cathy Watters, Marilyn Townsend, Gayle Baumgardner, and Joan Margolin, excavated skeletons as they were exposed by the construction crew. Upon uncovering a burial, the construction workers would suspend operations at that location until the skeleton could be removed by the archaeologists.

Throughout the six-day project, the volunteers concentrated on removing the bones while the author recorded excavation information and dug when possible. Some standard excavation procedures were not used because of the previous disturbance and limited time available. All horizontal control was based on the grid pattern on the contractor's blueprint rather than a site datum. Depth below surface measurements were not recorded since original land surface no longer could be determined. No attempt was made to screen soil from around the skeletons. However, several bulk samples of soil were taken from the graves. Photographs and field sketches were made; artifacts were recorded by individual burial when possible; and a burial orientation measurement was taken for each skeleton that was complete enough to warrant it.

#### SKELETONS

Ten skeletons were identified during the salvage excavation at the Harney site. Their locations are shown in Fig. 3 in relation to the grid pattern of footers and platforms. Numbers applied to the skeletons generally correspond to the sequence in which the burials were exposed. In Fig. 3, footers dug prior to the salvage project are distinguished from those dug during that project. Four skeletons (1,

2, 9, 10) were found beside previously dug trenches; five (3–7) were found in or adjacent to trenches dug during the salvage project; one (8) occurred outside the site grid.

Based on bones found to be articulated and in primary context when excavated, the minimum number of individual (MNI) skeletons identified during the salvage project was nine. Articulated remains were observed for one complete skeleton and eight incomplete ones. Some articulated bones from each of the eight incomplete skeletons were seen *in situ*, and it was apparent that the missing bones had been removed previously by bulldozers or picks and shovels.

In one case the archaeologists found bones that were *in situ* but were not articulated. These disarticulated bones, which were assumed to be from one individual (designated as skeleton 9), raised the MNI to ten skeletons recovered by the archaeologists during the salvage project. Identification of the ten skeletons was based only on those bones observed in context in the undisturbed areas of the site excavated by the archaeologists. Other bones from areas disturbed by the construction workers or bulldozers were not observed in context and thus did not count toward the MNI determined in the field.

*Skeleton 1.*—When first observed by the author, fragments of this skeleton were protruding into trench “M” from the west corner of platform “h” (Fig. 3). When excavated, the skeleton consisted of part of the innominate, some hand bones (resting on the hips), and the lower extremities, all articulated. The right tibia and the innominate were broken. Other bones, which were disarticulated, were found under and on both sides of skeleton 1. Fig. 4 shows the bones of skeleton 1 (#5, 6, 7) and the disarticulated bones (#1–4, 8–9) of at least one other individual (termed skeleton 9). The position of bone 4 of skeleton 9 is particularly illustrative because it underlies the right femur and extends beneath the pelvis of skeleton 1 (Fig. 4). The emplacement of skeleton 1 caused the disarticulation of skeleton 9 (see discussion under Skeleton 9).

*Skeleton 2.*—This skeleton was exposed by the construction crew at the same time the author was examining the materials from the paper sack. Part of the skull and broken long bones were lying in trench “I” east of platform “d” (Fig. 3). A mandible was observed *in situ* in the east wall of that trench, near where the footer ended. Most of skeleton 2 had been previously removed by the workers.

*Skeleton 3.*—Major damage had occurred to skeleton 3 before the author arrived at the Harney site. The skeleton was located in trench “G” between platforms “e” and “f,” where the previously dug footer ended (Fig. 3). These bones were well preserved, but all that remained were the lower extremities, from the distal ends of the femora (Fig. 5).

*Skeleton 4.*—This is the most complete skeleton excavated. It was found near the northeast corner of platform “e” in trench “I” (Fig. 3), in the part of the trench that was being dug while the archeologists were on the site. The skull was exposed in trench “I” and the rest of the body extended eastward, outside of the grid pattern. The cranium, which was collapsed and fragmented from the crushing weight of overlying soil (Fig. 6), was removed first because it was in the trench and liable to be damaged. When the post-cranial skeleton was uncovered, the vertebral column was seen to be slightly bowed and not in line with the lower extremities (Fig. 7). Skeleton 4 was fully articulated but the bones were flaking and rather friable. The skeleton had been placed in a pit dug into the rock stratum and displaced chunks of that rock were found resting on the skeleton and in the soil above.

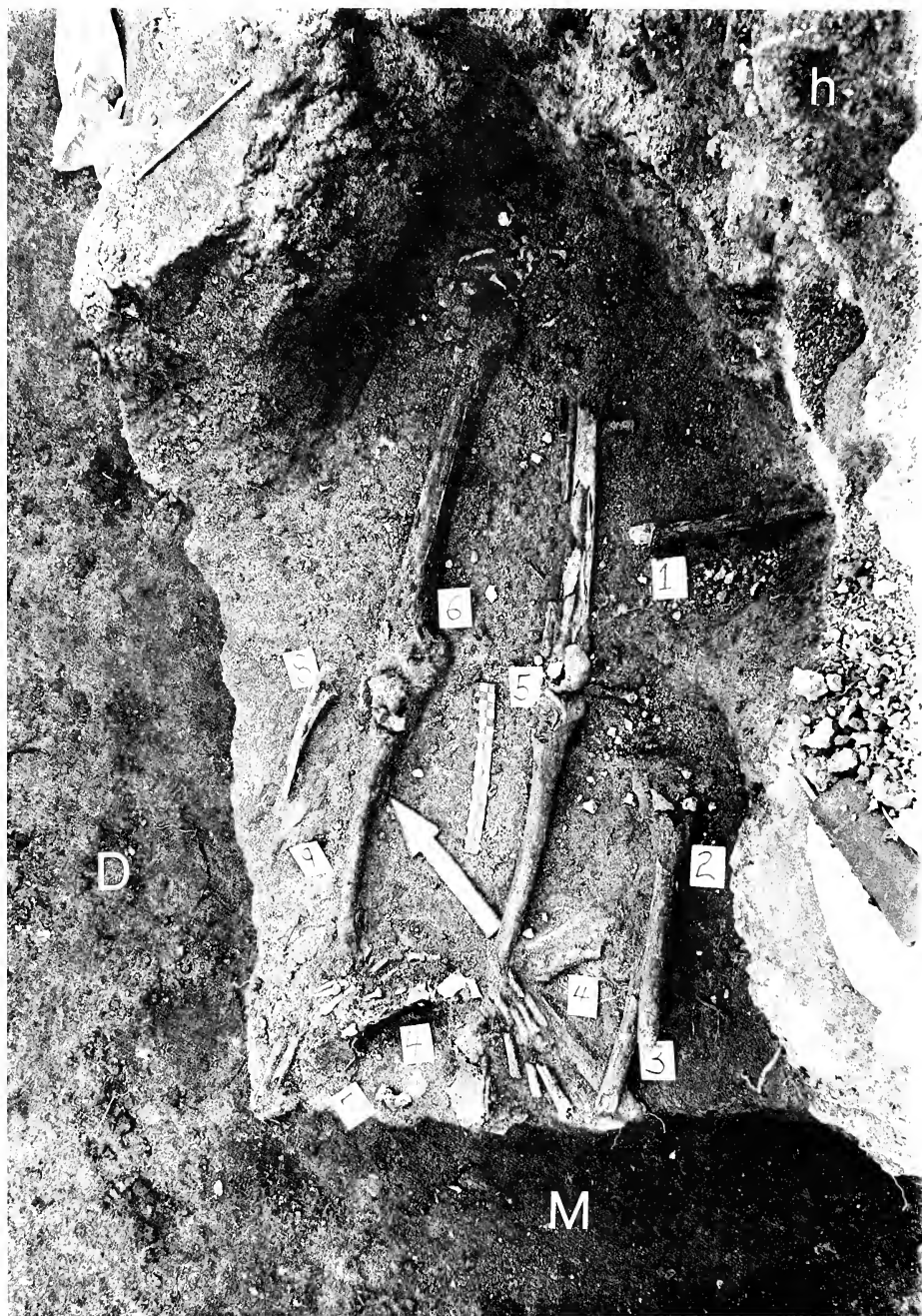


Fig. 4.—Skeletons 1 and 9 in the west corner of platform “h” at the intersection of trenches “D” and “M”. Bones 5–7 are from skeleton 1; bones 1–4 and 8–9 are from disarticulated skeleton 9. Skeleton 10’s lower leg bones were recovered later from the soil deposit in the upper left corner (under the pencil).



Fig. 5.—The lower extremities of skeleton 3. The white rock was positioned to support the left femur for the photograph.

*Skeleton 5.*—Skeleton 5, another partially damaged one, was found in a narrow pit east of platform “e” in trench “I,” not far from skeletons 3 and 4 (Fig. 3). It contained part of the vertebral column and upper extremities as well as the innominate and lower extremities (Fig. 8). The poor condition of the skeleton was





Fig. 6.—Collapsed skull of skeleton 4 found in trench “I.”

initially perplexing. The damage could not have been caused by picks and shovels because that part of trench “I” had not yet been dug by the construction crew. In this case, the damage probably was caused by a bulldozer blade dipping deeper at this spot while leveling the site’s surface.

*Skeleton 6.*—This skeleton was located near the intersection of trenches “C”



Fig. 7.—Post-cranial part of skeleton 4, with a bowed vertebral column that is not aligned with the lower extremities. This skeleton, the most complete one excavated, was placed in a shallow pit in the rock stratum.



Fig. 8.—Skeleton 5 found in trench “I.”

and “J” at the east corner of platform “b” (Fig. 3). Most of the bones had been removed by construction workers when trench “C” was dug before the salvage project began. When trench “J” was dug later, all that remained were fragments of various long bones that seemed to be articulated.

*Skeleton 7.*—Skeleton 7 was found at the intersection of a previously dug trench



("C") and a newly dug one ("L"). It was found on the south edge of platform "b" about 3 m away from skeleton 6 (Fig. 3). Again, part of the skeleton was removed during earlier construction work. Only the cranium was observed *in situ*. It was intact when first observed but broke into pieces when excavated.

*Skeleton 8.*—This partial skeleton was positioned about 10 meters outside of the grid pattern (Fig. 3). Lower leg bone fragments extended from the east wall of the pit dug for the swimming pool. The rest of the bones had been bulldozed.

*Skeleton 9.*—Bones of skeleton 9 and skeleton 1 were found in the same soil level of platform "h" beside trench "M" (Fig. 3). Skeleton 9 was not articulated; its bones were scattered on both sides of the lower part of skeleton 1 (which was articulated). Thus, the same undisturbed soil layer yielded part of an articulated skeleton and bones from a disarticulated one (Fig. 4). Although the scattered condition of skeleton 9's bones indicated the skeleton had been disturbed at some time, the disarray could not have been caused by the construction workers because their digging had been limited to the trenches and did not intrude into the platform. The soil layer in the platform was undisturbed when it was dug by the archaeologists.

Skeleton 9's bones were disarticulated and scattered in the historic past rather than recently. Skeleton 9 had been interred before skeleton 1. Gravediggers for skeleton 1, upon finding skeleton 9 already in place, pushed aside skeleton 9's bones to make room for the new burial. In doing so, they created the disordered condition of skeleton 9 that was observed upon excavation.

It is likely that some of skeleton 9's scattered bones were removed by the construction workers when they dug out the upper part of skeleton 1 in trench "M." An incongruous finding of mismatched bones in the opposite wall of trench "M" (in platform "l") supports this view. Fig. 9 shows part of a jaw (with an adhering clay pipe stem) found adjacent to a long bone.

*Skeleton 10.*—After skeletons 1 and 9 had been excavated, part of another skeleton was found nearby (Fig. 4). Skeleton 10 was located in the soil profile above skeletons 1 and 9. Only the distal ends of the lower leg bones of skeleton 10 were recovered. Most of the skeleton, which had been positioned in trench "D" beside platform "h" (Fig. 3), was removed by the construction crew before the archaeologists arrived.

### *Osteological Summary*

Subsequent osteological analysis (Mann et al., 1987) has established that 17 individuals are represented in the Harney site skeletal material. The discrepancy between ten individuals found during the salvage project and 17 skeletons identified during laboratory osteological analysis is due to the construction activity that occurred at the cemetery before the arrival of the archaeologists. The seven additional individuals were identified from the "multiple burial" bones dug by construction workers as well as other bones found by the author on bulldozer backdirt pile surfaces. None of these bones was observed *in situ* by the archaeologists. The osteological study also determined age, sex, and race estimates for some of the skeletons. Several individuals could reliably be raced as Black (Mann et al., 1987), and it was this determination, in combination with the artifact dates, that indicated the Harney site was a cemetery for Black slaves.

### BURIAL PATTERNS

Ubelaker (1978:13–18) indicates information should be recorded for a skeleton's location, deposition, position, orientation, and depth. Although some burial in-



Fig. 9.—The mismatched bones (long bone and jaw fragment) possibly belonging to disarticulated skeleton 9. A clay pipe stem fragment (see arrow) rests beneath the jaw.

formation was secured for most skeletons, it was not possible to record complete information for all skeletons at the Harney site because of disturbance at the cemetery, the partial condition of most skeletons, and limited time available. Information on deposition, position, and orientation is presented below; location

Table 1.—Orientations of articulated skeletons at the Harney site. All are "west-headed" interments.

Skeleton	Azimuth (magnetic)	Measurement taken at
1	243°	femora
3	250°	femora
4*	270°	vertebral column
	281°	femora
5	256°	femora
8	263°	tibiae

\* Legs and vertebral column were not aligned.

information has been presented above; no measurements for depth below original land surface were possible because of previous removal of the overburden.

### *Deposition and Position*

Six of the nine articulated skeletons (1, 3, 4, 5, 8, 10) were confirmed to have been interred lying on their backs. Whether the other three articulated skeletons (2, 6, 7) or the disarticulated one (9) were emplaced on their backs could not be established because too few bones were observed *in situ*.

Position of the legs in relationship to the trunk could be determined with certainty in only three skeletons (1, 4, 5), each of which retained at least part of its pelvis. Legs fully extended from the pelvis in each instance. For skeleton 3, the junction of the remaining distal parts of the femora with the tibiae suggests its legs probably were fully extended as well (Fig. 5).

Position of arms with respect to the trunk was observed for the same skeletons (1, 4, 5) as the legs. The hands of skeletons 1 and 5 rested on their respective hip (Figs. 4, 8). The right hand of skeleton 4 rested on its right hip but the left hand was centered on the pelvis (Fig. 7). In no instance did hands actually cross over one another on the pelvis.

### *Orientation*

The direction in which the body was interred was established for eight articulated skeletons excavated at the Harney site. Direction was based on placement of the legs alone in six cases (1, 3, 5, 6, 8, 10), of the skull alone in one case (7), and of both legs and skull in one case (4). Legs consistently pointed toward the east, while the top of the skull, in the two observed cases, was positioned toward the west. Handler and Lange (1978:161) refer to this as the "west-headed" direction.

Azimuths were taken for five skeletons that were complete enough to allow for measurement. Orientations of those five skeletons are shown in Table 1. Most measurements were taken between femora or tibiae because the upper parts of the skeletons had been removed. Two azimuths were taken for burial 4 because the vertebral column and legs were not aligned (Fig. 7). Azimuths range from 243° to 281° with most being slightly south of west.

Neither direction nor azimuth could be determined for skeleton 9, the disarticulated one, or for skeleton 2, an articulated one having few bones observed *in situ*.

### *Burial on "Shoal"*

The author observed bone fragments protruding from the walls of some platforms during his first visit to the Harney site. These fragments occurred at the top of the rock stratum at the base of the soil layer. When the articulated skeletons



Fig. 10.—The marked contrast between the white rock ("shoal") below and the grey soil above is evident near skeleton 2. Skeletons found *in situ* had been consistently buried at the interface of these strata.

were excavated, bones were again observed to rest atop the rock. A pattern of interment at the interface of these two strata was consistent across the site. Persons who originally dug the graves made it a practice to dig through the soil layer to the rock stratum before interring the body. In a few instances, narrow and shallow burial pits were dug into the top of the rock stratum. Chunks of this displaced rock were found adjacent to and resting on the skeletons in several burials as well as in the fill above.

Fig. 10 shows that the grey, friable soil contrasts markedly with the white, compacted rock stratum, which is locally called "shoal." This term has been used in several ways in the past. Hardy (1922:191) uses *shoal rock* to refer to fragmental volcanic material that has been consolidated into agglomerates, breccias, and tuffs and then exposed on the surface of the land. His *shoal soils* "are typical sedentary soils, for they have been derived from consolidated fragmental rocks which they usually directly overlie" (Hardy, 1922:193). Later (Hardy et al., 1949:9–10), the terms *geological shoal* and *pedological shoal* are substituted, with the latter classed as a hydromorphic soil that is subject to drainage impedence, hard cementation ("resembles concrete"), and development of a characteristic clay type of soil. A more recent study of Montserrat's soils places shoal soils in the widespread Smectoid Clays category (Lang, 1967:15–17).

Conversations with the contractor and construction crew established the fact that their use of the term "shoal" referred to the rock stratum upon which the burials were found. Samples of this consolidated material and the overlying soil near skeleton 2 were submitted for X-ray diffraction analysis and microscopic observation. The report, "Analysis of soil and rock from Montserrat" (by G. A. Cooke, 1986; unpublished report on file at Division of Anthropology, The Carnegie Museum of Natural History) identifies the rock sample as "... a partially welded tuff composed of trydimite/cristobalite, anorthite, magnetite, amorphous silica and quartz" (p. 3). This finding confirms the tuff identifications of MacGregor (1939:39) and Martin-Kaye (1959: fig. 12) for the Bransby Point area. The report also states (p. 2): "The mineralogy of this soil is entirely consistent with a weathered ash. The lack of a well developed smectite indicates a Late Pleistocene to Recent age." Mineralogical similarities between samples of soil and tuff indicate this tuff, or one very similar to it, is the parent material for the soil.

### *The Coffin Issue*

The presence of nails (see discussion under Artifacts) suggested that interment in coffins may have been another burial pattern at the Harney site. The possibility of coffin interment was recognized early in the project when seven nail fragments were found in the paper sack.

Efforts to clarify the coffin issue took two forms. Initially the author examined areas around the bones that protruded from the platform walls for evidence of coffins. During subsequent excavation of the *in situ* burials, the volunteers were especially attentive to any indicators of coffin remains.

Nails found in the graves continued to be the only indicator of possible coffin interment at the Harney site. Nails were found adjacent to and in the fill above five skeletons (3 females, 2 males; Mann et al., 1987: table 1). Despite careful observation of the platform walls and graves, no fragments of coffin wood, no discolored or stained soil from decomposed coffins, and no coffin hardware such as handles were found.

The issue of coffin burial at the Harney site remains a perplexing one. If one

Table 2.—*Distribution of artifacts by excavated burial.*

Burial <sup>a</sup>	Nails <sup>b</sup>	Pipe stem	Colonoware	Imported pottery	Metal disc	Total
1 (+9?)	33 (17)	1	8	—	1	43
3	13 (9)	—	1	—	—	14
4	—	1	—	—	—	1
5	32 (12)	—	—	—	—	32
6	—	—	1	—	—	1
8	4 (0)	—	—	1	—	5
10	7 (2)	—	—	—	—	7
	89 (40)	2	10	1	1	103

<sup>a</sup> No artifacts in burials 2 and 7.

<sup>b</sup> Fragments first; nail heads (MNI) in parentheses.

accepts the occurrence of nails as suitable evidence for the presence of coffins, then coffin burial took place in at least five of the excavated graves. Occurrence of coffins would be a reasonable explanation for the presence of the nails in those five graves. It is difficult to account for why else nails would be found.

Barring a reasonable alternative explanation for the presence of nails, it seems logical to conclude that coffins, or some kind of burial apparatus (e.g., planks) requiring nails, were used in some graves at the Harney site. Handler and Lange (1978:150), in their work at Newton Plantation, Barbados, used the presence of nails to indicate occurrence of coffins when other evidence was absent. Yet, in some graves they did find additional hardware, such as coffin handles, that verified use of coffins at Newton Plantation. At the Harney site, the presence of coffins or other burial apparatus cannot be independently corroborated because we found no coffin wood, other coffin hardware, or even discolored soil.

### ARTIFACTS

A total of 134 artifacts were recovered from three locations at the Harney site—the graves, paper sack, and backdirt piles. The range of artifacts includes nails, other metal items, clay pipes, “colonoware” pottery, imported earthenware and stoneware ceramics, and glass.

#### *Artifacts by Burial*

Only those artifacts found in excavated graves can be related to the ten burials. Of the 134 artifacts recovered, 103 (77%) are from graves. Although some artifacts occurred in proximity to the bones, others were recovered from soil above the skeletons and may have been unintentionally included when the graves were being filled. It is not certain that any of these artifacts were purposefully deposited as grave goods to accompany the deceased.

Table 2 presents the distribution of artifacts by burial. Seven of the ten burials had artifacts; two burials with incomplete skeletons (2, 7) had no artifacts; if there were artifacts from burial 9 (disarticulated skeleton), they could not be distinguished from those for burial 1. Of the seven burials with artifacts, two (4, 6) had only one artifact apiece. The fact burial 4 has but one artifact is of special note because that grave contained the skeleton that was most complete when excavated.

#### *Nails*

Iron nails found in the excavated burials are all heavily corroded. No attempt was made to measure the nails because of the corrosion, but it is worth noting



that there does appear to be variation in both length and diameter among the whole nails. No effort was made to determine the shape of a nail head because it is a rusted lump without clear form. These seem to be wrought rather than cut nails.

The 89 nail fragments are by far the most abundant artifact (86%) from the burials (Table 2). There are 40 nail heads, each representing an individual nail, while the other fragments are broken shanks.

Nails were found in five of the excavated graves (1, 3, 5, 8, 10). In Table 2, some of the 17 nails attributed to skeleton 1 may have been originally associated with disarticulated skeleton 9. However, two nails found immediately adjacent to the right knee and lower tibia of skeleton 1 can be reliably associated with that skeleton. The partial skeletons from the other four graves, all of which were individual interments, yielded a wide range of nails (Table 2). Mann et al. (1987) found one nail adhering to the left femur of skeleton 10.

Nails were not found with three of the incomplete skeletons (2, 6, 7). Their absence may be due to the fact that very few bones remained *in situ* when the archaeologists arrived because the construction crew already had removed most of the skeletons. However, the same logic does not apply to burial 4, which also yielded no nails. Absence of nails in that grave cannot be attributed to the construction workers' action since the skeleton was complete when excavated by the archaeologists. In the case of skeleton 4, the lack of nails implies that this individual originally was interred without a coffin.

### *Pipe Stems*

Pieces of clay pipe stem were recovered from two excavated burials (1, 4) both of which were females (Mann et al., 1987: table 1). One tapering piece (length = 57.1 mm; maximum diameter = 6.3 mm) from the rear of the stem was found with skeletons 1 and 9. It has a stem hole diameter of 4/64ths of an inch. A second stem fragment, shorter but thicker (length = 41.8 mm; maximum diameter = 9.3 mm), was the sole artifact found with skeleton 4. Its stem hole diameter is 5/64ths of an inch. Both stem hole diameters predominated during the eighteenth century (Noël Hume, 1969c:298). No pipe bowls were found in the excavated graves.

### *"Colonoware Pottery"*

Ten small sherds from three burials at the Harney site have been labeled "colonoware," a term that implies the pottery was made locally and probably by slaves, although that is not certain.

Three distinct vessels have been identified. One vessel, based on one body sherd, occurred in burial 6. Another vessel, also based on a single body sherd, was found in burial 1. The third vessel is of special interest because seven of its sherds (one rim, six body) were found with burial 1 while one body sherd occurred with burial 3. Colonoware sherds were found with male and female skeletons.

The vessels are coil constructed with generally well finished surfaces but without decoration. Sherds are predominately gray or brown but there is considerable variation in color even for a single sherd. This reflects a reduced firing environment with typically fast cooling. Temper is principally derived from a sort of quartz dominated composite. Hornblende is also present as are limestone and grog in lesser amounts.

It is unlikely these sherds are the broken remnants of purposefully placed grave goods because most were found in the fill overlying the skeletons. Also, sherds from the same vessel were found in two separate burials (1 and 3) located some

Table 3.—*Distribution of disturbed artifacts.*

Location	Nails <sup>a</sup>	Pipe stem	Pipe bowl	Colonoware	Imported pottery	Glass	Other metal	Total
Sack	7 (3)	4 <sup>b</sup>	1	—	—	1 <sup>c</sup>	—	13
Backdirt	<u>—</u>	<u>—</u>	<u>1</u>	<u>9</u>	<u>6</u>	<u>1</u>	<u>1</u>	<u>18</u>
	7 (3)	4	2	9	6	2	1	31

<sup>a</sup> Fragments first; nail heads (MNI) in parentheses.  
<sup>b</sup> Includes pipe stem found with jaw and long bone.  
<sup>c</sup> Turlington phial.

10 m apart. A more plausible explanation is that the sherds were unintentional introductions into the graves when they were filled.

*Imported Ceramics*

A single unglazed earthenware body sherd was found beside skeleton 8 in the wall of the pit dug for the swimming pool. This sherd has been separately classed because it is distinctly different from the “colonoware” pottery. The earthenware sherd is red (2.5YR5/8), thick (about 13 mm), and has a uniformly fine-grained paste. Utilitarian earthenwares of this sort were imported into the West Indies in great quantity. Such sherds are commonplace in plantation sites.

*Metal Disc*

An unusual object found in the fill above skeletons 1 and 9 is a metal disc somewhat ovoid in shape. The maximum diameter is 23.8 mm; the minimum diameter is 21.4 mm; the thickness is 0.6 mm. Green patination on its surface indicates the disc is a copper alloy. The item’s shape at first suggested it might be a coin, but subsequent microscopic examination revealed there was no inscription visible. Its sheared edge indicates the disc was cut and its surface appears to be hammered. It does not appear to be a coin or a button. The function of the artifact remains uncertain.

Handler and Lange (1978:201) note that a Barbadian document refers to the practice of putting coins over the eyes of the deceased. They did not find any examples of this practice among the Newton Plantation skeletons. Although it is possible that the Harney site disc was meant to function as an eye covering, this seems unlikely since the item was not found with skeleton 1 or 9 but instead in the fill above.

*Disturbed Artifacts*

Thirty-one artifacts, which had been removed from primary context by the construction crew or bulldozer, were collected by the author during the project. The paper sack contained 13 of these artifacts. Discussion with the crew revealed that these artifacts had been found with various bones in different trenches. Another 18 artifacts were collected by the author from backdirt piles created when the site surface was leveled by bulldozers. Table 3 shows the distribution of artifacts from the sack and backdirt piles. Discussion about these disturbed artifacts is limited because they cannot be definitely associated with particular skeletons.

Three clay pipe stem fragments and one bowl were found in the sack. A fourth stem fragment, found with the mismatched jaw and long bone (see discussion under Skeleton 9), fits with one stem from the sack. All pipe stem hole diameters are 4/64ths of an inch. The pipe bowl from the sack has no heel but does have



raised relief on the front and back of the bowl in the form of a branching stemmed device. The relief vaguely resembles that on a pipe bowl found at Newton Plantation (Handler and Lange, 1978: fig. 37). The bowl is scorched very little from smoking. A heavily charred pipe bowl from the backdirt pile is plain and lacks a heel. There are no markings on any of the pipe fragments indicating the name or location of the maker.

The one rim and eight colonoware sherds from the backdirt piles, which are very similar to the ones excavated, have somewhat more variation in color but the surface and temper are almost identical. The nine sherds come from at least four vessels. These are four different vessels from the ones identified from excavated colonoware sherds.

Six sherds of imported ceramics came from bulldozed backdirt piles. The paste (color and texture) in one body sherd is very similar (apart from a gray core) to the earthenware sherd found with skeleton 8, but the exterior is black glazed. It resembles the Buckley pottery of North Wales described by Noël Hume (1969c: 133). The second earthenware piece is an unglazed reddish yellow (5YR6/6) rim with a gray core. Two body sherds of tin-enamelled decorated delftware, one with the remnant of a cobalt blue design and the other with manganese purple and cobalt blue (Noël Hume, 1969c:106), were found in the backdirt piles. The fifth earthenware piece is a thin, plain creamware body sherd. The sixth sherd is stoneware with a light red (2.5YR6/6) and ribbed interior, gray to cream paste, and brown-mottled exterior. The shiny exterior, which lacks the pitting associated with salt-glazed ceramics, suggests this may be Nottingham stoneware or a similar variety (Noël Hume, 1969c:114). All of these ceramics were in production for at least part of the eighteenth century (South, 1977: table 31).

One intact glass phial was found in the paper sack. One straight sided, thick (7.9 mm) fragment of green glass and a corroded, wedge-shaped metal object (possibly a shim) were recovered from the backdirt piles.

#### *"Missing" Artifacts*

One category of artifacts that might be expected to be present in the burials was not found. No buttons, pins, or other clothing accoutrements were recovered. It is possible that some of these materials, which might have originally accompanied the corpse to the grave, decomposed over the years. Mann et al. (1987) found some evidence to support this notion for two female skeletons (2, 4) in the form of green copper salts stains that suggest use of a pin or ornament. It is also possible that the corpses were interred in shrouds, which do not necessarily require pins or other fastening devices, or naked.

A second category of absent artifacts includes those of African origin or derivation. Several artifacts of this kind were found in the Newton Plantation graves on Barbados (Handler, 1981; Handler and Lange, 1979). No such artifacts were found at the Harney site.

#### THE TURLINGTON BALSAM OF LIFE PHIAL

Preliminary information on the Turlington Balsam of Life phial from the Harney site has been presented previously (Watters, 1981). That paper described the phial and compared it with a similar bottle found in the "abortive well" near Wetherburn's Tavern in Williamsburg, Virginia (Noël Hume, 1969b:34). The author had not seen the Williamsburg bottle before publication of the 1981 paper and, therefore, was uncertain whether the Montserrat artifact was an authentic

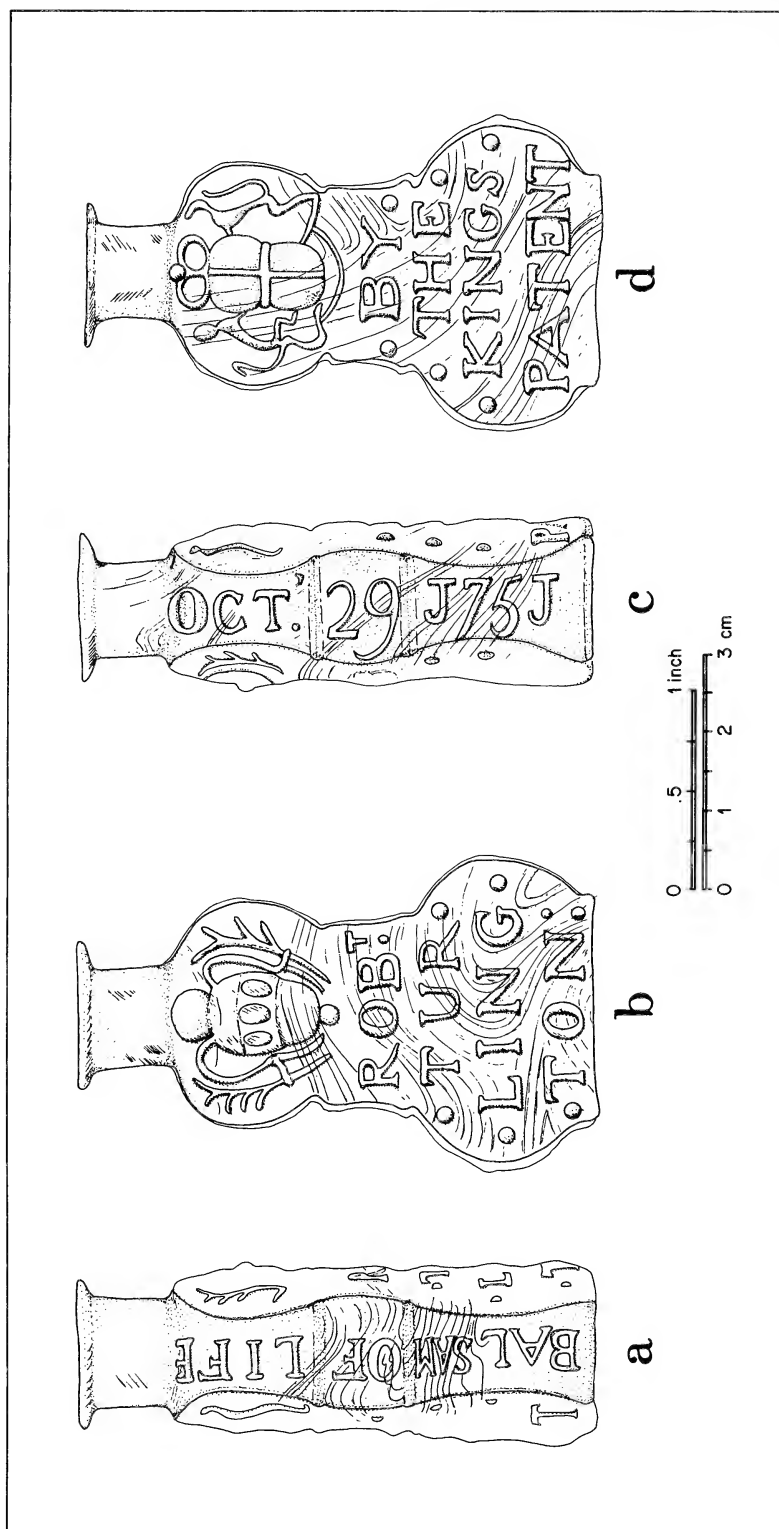


Fig. 11.—Four views (actual size) of the “cello-shaped” Turlington Balsam of Life phial (clockwise rotation sequence).

Turlington Balsam of Life phial or one of the many counterfeit bottles produced in the mid 1700s. In 1982, the author had the opportunity to observe the Wetherburn's Tavern bottle and compare it to the Montserrat phial. It was evident the two bottles basically were very similar, apart from the date, and that both were well crafted in comparison to counterfeits. For these reasons, the Montserrat phial is now regarded as another genuine Turlington bottle.

#### *Location and Recovery*

The Montserrat phial was first observed by the author as one of the artifacts contained in the paper sack that had been buried in another part of the Harney site by the construction workers. Interviews with the workers revealed that the bottle had been found near the intersection of trenches "D" and "M" at the west corner of platform "h" (Fig. 3). They recalled the location where they found the phial because it was intact and therefore noteworthy, which aroused their curiosity. The bottle was found in the soil above the shoal stratum but its exact location in the soil profile was not remembered. It is remarkable the bottle was not shattered by picks or shovels as the soil and shoal were being dug from the trenches.

Portions of three skeletons (1, 9, 10) eventually were excavated at the west corner of platform "h." Part of each skeleton had been removed when the two trenches were dug by construction workers; in addition, the bones of skeleton 9 already had been disarticulated in the historic past. Although it is logical to conclude that the Turlington bottle originally was emplaced, whether intentionally or not, with one of these three skeletons, it is unlikely we will ever know with which one in particular.

#### *Turlington's Balsam of Life*

Robert Turlington patented his "Balsam of Life" in Great Britain in 1744 and the patent medicine, which contained no less than 27 ingredients, soon became quite popular (Griffenhagen and Young, 1959:160). Its success quickly attracted some unscrupulous competitors, whose actions caused numerous problems for Turlington. These competitors bought used Turlington bottles and filled them with spurious material for resale; eventually they began to produce counterfeit bottles bearing Turlington's name (Noël Hume, 1969c:74). Turlington's efforts to thwart competitors appear to have been unsuccessful for the most part.

The Williamsburg bottle, which is dated MARCH 25 or 26 1750 (a crack obliterates the questionable digit), is the earliest known example of Turlington's proprietary bottle. It is the "cello shaped" variety (Noël Hume, 1969a: fig. 38; 1969b: fig. 24). The Harney site phial, dated OCT 29 1751, is also cello shaped (Fig. 11). The dates and other raised inscriptions on the bottles were imparted by the molds into which the glass was blown. The fact that these two almost identically shaped bottles were made in different molds and have dates that are only twenty months apart may represent an effort by Turlington to authenticate his product by changing production dates on his phials. If so, the practice apparently was not successful because Turlington eventually altered the shape of the bottle itself in 1754 to one with a distinctly angular form (Jones and Smith, 1985: Fig. 115). Notwithstanding Turlington's efforts, his competitors were soon producing angular-shaped counterfeit bottles (Noël Hume, 1969a: fig. 39).

#### *Comparison*

The Wetherburn's Tavern and Harney site phials are similar in many ways. Both are of swirled, clear glass. The "... crude rendering of the British royal arms



Fig. 12.—Details (enlarged) of the British royal arms (corresponds to Fig. 11d).

and their supporters . . .” (Noël Hume, 1969*b*: fig. 24 caption) above the words BY THE KINGS PATENT occurs also on the Montserrat phial (Fig. 12).

An embellishment on the reverse side of the Montserrat phial is difficult to discern clearly, but it may correspond to the shield with three pear-shaped devices described by Noël Hume (1969*b*: fig. 24 caption) for the Wetherburn’s Tavern bottle. The embellishment seems to be a shield having three projections arranged horizontally across its center (Fig. 13). Above the shield and articulating with it is a rounded projection. A raised, curved device encloses the shield on each side and joins the projection above and almost touches yet another projection below the shield. Branch-like emblems join the curved device on each side. Beneath the shield are the words ROBT TURLINGTON.

Both phials have the words BALSAM OF LIFE arranged along the curves on one edge. On the Harney site bottle the letters BAL are somewhat larger than SAM and the latter appear to be somewhat compressed (Fig. 12, 14). The Williamsburg bottle has letters of more equal size.

The other edge of each bottle has its date. Although the dates are different, the arrangement of letters and numbers, with the month, day, and year fitting into the curves of the bottle’s edge, is the same. The numeral “1” is decidedly J-shaped and numerals “9” and “7” have tails on the Montserrat phial (Fig. 15).

Apart from the date, there are a few other differences between the two bottles including the rendering of the lip, symmetry of the shoulders, and arrangement



Fig. 13.—Details (enlarged) of the shield with three pear-shaped devices (corresponds to Fig. 11b).

of various projections around specific words (Watters, 1981:107). All of these are variations specific to a mold.

There is a slight variation in height between the Williamsburg and Montserrat bottles. The lip to base measurement for the Montserrat phial is  $2\frac{17}{32}$  inches. The Williamsburg bottle (excluding the slightly projecting pontil) measures  $2\frac{3}{4}$  inches (based on a remeasurement made in 1980 by Noël Hume to whom I am indebted; see Watters, 1981:107, for a discussion of other heights given for the Wetherburn's Tavern bottle).

There is some variation in details of the Montserrat phial depicted in the illustrations accompanying this paper. Certain parts of the phial showed considerable wear and that tended to obliterate some of the details or make them difficult to discern. Also, Fig. 11 was drawn from the bottle itself by one illustrator, whereas Fig. 12–15, drawn by another person, were based on prior illustrations and photographs since the bottle itself already had been returned to the Montserrat National Trust, where it has been displayed in the museum since 1983.

The Montserrat and Williamsburg phials are examples of authentic Turlington bottles that are noteworthy because of their overall similarity in form and inscription. The minor differences between these two bottles can be attributed to variation in the molds. The difference that is most intriguing is the twenty month separation in mold dates, especially if it really indicates Turlington's effort, albeit apparently unsuccessful, to block the actions of his unscrupulous competitors.



Fig. 14.—Details (enlarged) of the BALSAM OF LIFE lettering (corresponds to Fig. 11a).

## DISCUSSION

### *The Cemetery Site*

The existence of a cemetery at the Harney site was first revealed by the excavation work for the house foundation. According to the contractor and construction workers, the surface of the site contained no indications of this unmarked and unrecorded cemetery. It was only after they began to dig the trenches and encountered bones that they suspected the presence of human burials.

Historic structures are not found in the immediate vicinity of the cemetery. The closest historic buildings are located about 500 m north of the Harney site. A recent map of Montserrat (Directorate of Overseas Surveys, 1978) shows these structures as “building remnants” (UTM coordinates NP819488). It is possible they represent the remnants of the Bransby Plantation, noted on earlier historical maps of Montserrat, although that is uncertain. It also is uncertain that the cemetery is related to those buildings. Other historic structures may occur in the general vicinity of the Harney site, but, because of time constraints, no systematic survey was conducted to investigate their occurrence.

One intriguing development occurred about four months after the Harney site excavations. In October 1979, the Montserrat National Trust found the remains of a gun battery including stone fortifications and the guns themselves at the tip



Fig. 15.—Details (enlarged) of the OCT 29 1751 date (corresponds to Fig. 11c).

of Bransby Point (Fig. 1) about 1.2 km WNW of the Harney site. This discovery raised the possibility that the Harney site skeletons may have been those of soldiers or militiamen killed during one of the attacks against Montserrat, perhaps one of several raids made by the French.

The possibility of the skeletons being soldiers added to the list of other possibilities that included Black slaves, White indentured servants, and freedmen. All were present on Montserrat during the colonial era. Indentured servants, especially Irish, were present in considerable numbers but later were largely replaced by Black slaves (Pulsipher, 1977). The lack of burial accoutrements and the unmarked nature of the graves suggested that the burial ground probably was not for plantation owners or managers. However, if the deceased had died during an epidemic and been hurriedly buried, then it is possible that the skeletons were of those of plantation managers. Given the range of possibilities, an analysis by physical anthropologists was needed to answer these questions.

Osteological study (Mann et al., 1987: table 1) has now shown that the two skulls recovered (4, 7) from the *in situ* burials are definitely from Black individuals. Two bones from the disturbed "multiple burial" are identified as Black (one is provisionally identified). Race was not determined for post-cranial skeletons from *in situ* burials or for the other disturbed bones. They are simply listed as "race indeterminate" (Mann et al., 1987: table 1). Although it is likely that all the

skeletons from the Harney site are Black individuals, that is not certain. The possibility remains that at least some are White individuals.

The designation of these individuals as slaves rather than freedmen is primarily based on the most likely time of use of the Harney site cemetery in the latter eighteenth century, before slavery was abolished in the British West Indies. The 1751 date inscribed on the Turlington Balsam of Life phial provides the most secure date for use of the cemetery. Although the bottle obviously could not have been placed in the grave prior to its manufacture in 1751, it could have been emplaced any time thereafter. It most likely was deposited quite some time after 1751 because of the lag time between production in England and shipment to the West Indies. How the Turlington bottle ultimately came to be placed in a slave's grave is an intriguing question that probably never will be answered.

The Turlington phial is the only artifact bearing a date. However, there are two other categories of artifacts that support the view that the cemetery was used in the latter eighteenth century. One pipe stem from an *in situ* burial has a bore diameter of 5/64ths of an inch; the second *in situ* pipe stem diameter is 4/64ths of an inch. The former size predominated in the first half of the eighteenth century and the latter in the second half. Four pipe stems and two pipe bowls from the sack and backdirt piles also have 4/64ths inch diameters. Since the four stems and two bowls were found out of context, they cannot directly support the argument for a latter eighteenth century use of the cemetery. However, they are in accord with and do not contradict the findings for the pipe stems found *in situ*. The imported ceramics, for which manufacturing ranges are known, were all produced for at least part of the eighteenth century. Again, this is only indirect support because they were found out of context.

The six-day project was able to salvage remains from 17 individuals, but it is unlikely that this represents the total skeletal population buried at the Harney site. The distribution of recovered skeletons (Fig. 3) tends to cluster around platforms "b, h, and d-e." However, this is because archaeological work was restricted to the confines of the house foundation and, apart from the swimming pool, areas outside were not investigated. The probability that additional burials still exist at the Harney site is high because much of the potential burial area was not tested. Since the now completed house stands on the site, the possibility of further testing is limited.

### *Correlations*

The Harney site skeletons are the only slave skeletons known from Montserrat. Burials of prehistoric Amerindians have been found on occasion, the most recent of which was within the confines of the capital of Plymouth a few years ago.

Significant work on plantation archaeology has been underway at Galways Plantation, located in southwest Montserrat on the slope of the Soufrière Hills (Fig. 1). Pulsipher and Goodwin (1982:83-85) mention that two burying grounds may have been identified at Galways. One presumably is for Whites because it has headstones. The other, which consists of mounded piles of rocks, was thought to possibly contain slave burials. More recently, further research (Goodwin, 1987: 95-104) has been carried out in the slave village at Galways. Goodwin (personal communication 1987) suspects the rock mounds do not contain burials but instead were erected by small plot cultivators in later years. If that is the case, then the location of the Galways slave burial ground remains to be discovered. Work at Galways planned for the summer of 1987 may help resolve the issues related to its cemeteries.



Although studies of plantation archaeology have occurred elsewhere in the Caribbean, such as Armstrong's (1983, 1985) work at Drax Hall, Jamaica, the research generally has not included excavations of slave cemeteries. On the other hand, skeletons of West Indian Blacks have been exhumed inadvertently on occasion. Ubelaker and Angel's (1976) brief report on two Black skeletons from St. Thomas, U.S. Virgin Islands, essentially falls into this category.

The most significant study on Black slave burials in the West Indies is on the Newton Plantation site on Barbados. That study used historic documents and archaeological field research to provide a broad-based background on slave life in Barbados (Handler, 1972; Handler and Lange, 1978, 1979). Much of the earlier work focused on information that could be gained from analysis of the cemetery site, burial patterns, and artifacts in conjunction with historic documents (Lange and Handler, 1985).

More recently, the skeletal material has been examined from physical anthropological perspectives to gain information about the health, diet, and diseases of the slaves (Corruccini et al., 1982; Handler and Corruccini, 1983). While some studies have dealt with quite specific topics, such as tooth mutilation (Handler et al., 1982), others have more general intent, such as evidence for weaning (Corruccini et al., 1985; Handler and Corruccini, 1986). One of the most interesting revelations is the recent discovery of high lead content among Newton Plantation skeletons, which apparently resulted from consumption of rum contaminated by lead parts used in plantation distilleries (Handler et al., 1986).

The total number of individuals recovered from the Newton Plantation site is 104 (Corruccini et al., 1985), which is 12 more than originally reported (Handler and Lange, 1978), three more than reported after the first physical anthropology study (Corruccini et al., 1982) and about six times greater than for the Harney site where 17 individuals were identified (Mann et al., 1987). The interment period at Newton Plantation extends from about 1660 to 1820. At the Harney site, burials probably took place in the latter eighteenth century (possibly longer), which is a much more restricted timespan.

There are interesting similarities between the populations. At Newton Plantation, west-headed orientation predominated although skeletons with east and rarely north orientation were also found (Handler and Lange, 1978:161). Of particular interest is the stratigraphic and artifactual evidence that indicates west-headed interments at Newton Plantation tended to occur more recently than the east-headed ones. In general, the Barbados data show that the more recent the burial, the more likely it was to be oriented toward the west. The Harney site graves, which would correspond to the later part of the Newton Plantation burial timespan, would be expected to yield skeletons emplaced in a west-headed direction. At the Harney site, the orientation was west-headed for eight burials; two others could not be determined.

Also of interest, confirmed coffin burials at Newton Plantation were all west-headed (Handler and Lange, 1978:163). At the Harney site, the five corpses that may have been interred in coffins were all west-headed. Bodies were placed on their backs with legs extended at the Harney site; most bodies from Newton Plantation were also interred that way.

For adult skeletons at the Harney site that could be sexed, the ratio of males to females is about even. Four subadults were identified; no fetal or infant skeletons were found. Overall, males appear to have died at earlier ages than females. Mann et al., (1987) discuss age, sex, race, and stature estimates as well as paleopathological conditions in detail.

Apart from nails, relatively few artifacts were found with the *in situ* burials (Table 2) at the Harney site. Although some artifacts were found near the skeletons, others were found in the fill above. Because it is not certain that any one of these objects was purposefully emplaced with the deceased, it is better not to regard them as grave goods *per se*. Handler and Lange (1978: table 16) record a wider variety of artifacts from Newton Plantation burials. However, in general they note that "very few grave goods were encountered at Newton . . ." (Lange and Handler, 1985:26), and those found were mainly glass beads and clay pipes. A major difference was that artifacts of African origin or derivation were found at Newton Plantation but not at the Harney site.

Burial in mounds, a mortuary pattern that was identified at Newton Plantation, cannot be addressed at the Harney site because the surface had already been bulldozed before the archaeologists arrived. A second Newton Plantation mortuary pattern, family burial plots (Corruccini et al., 1982:446), seems related to the existence of the mounds and, therefore, also cannot be addressed at the Harney site.

In summary, some of the burial patterns, including west-headed orientation, arrangement of corpses on their backs, paucity of artifacts, and possible interment in coffins for some burials, exist at both the Harney site on Montserrat and the Newton Plantation on Barbados. The practice of burying the corpse atop the shoal stratum at the Harney site would be a site-specific phenomenon due to the geology of the Bransby Point area. The Harney site was used as a cemetery at least in the latter eighteenth century and its burial patterns seem to correspond to the later burial timespan at Newton Plantation.

#### ANTHROPOLOGICAL OBSERVATIONS

During the course of the archaeological excavations at the Harney site, we observed several behavioral patterns among the construction workers that are of passing interest. None of the workers would actually touch the skeletal remains we excavated. In the one instance when a worker did bring us a bone, he did not actually touch the bone but instead had it suspended from a thin loop of vine. Their decided reluctance to handle bones most likely derives from the persistence of *obeah* (magic) practices on Montserrat (Dobbin, 1983:26–31). The workers' concern was as much for our well-being as for theirs.

There is no doubt that the workers initially were uneasy about us working at the site. Eventually, however, they displayed great interest in the work we were doing and understood the careful excavation techniques used, once we explained why these methods were important. Jackie Dangler was the person most responsible for allaying the workers' initial concern about our activities because he was the foreman as well as a former medic. Although they became used to the idea that we could work together without harm during the day, the workers expressed considerable worry about my well-being when I stayed alone at the site several evenings to continue the excavations. Having been advised to be wary of the spirits, I suspect my decision to continue working after the construction crew left at the end of the workday was viewed as foolhardy.

Undoubtedly the most interesting activity occurred the day after we completed the excavations. I brought a bottle of rum to the site to share with the workers in appreciation of the assistance they had given to us during the project. I was very intrigued when, before any of us partook, Jackie Dangler walked to the house foundation and sprinkled small amounts of rum into the trenches where we had

found the skeletons. He and the construction crew expressed their satisfaction that now since "they" (the spirits) had partaken, we could enjoy the remainder of the rum. This activity was interesting in its own right, but I later became even more intrigued when I read a statement (cited in Handler and Lange, 1978:199) concerning the practice of spilling rum on a slave's grave, based on an observation made in Jamaica in 1707.

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DESCRIPTION OF SKELETAL REMAINS FROM A  
BLACK SLAVE CEMETERY FROM  
MONTSERRAT, WEST INDIESROBERT W. MANN<sup>1</sup>LEE MEADOWS<sup>1</sup>WILLIAM M. BASS<sup>1</sup>

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## ABSTRACT

The skeletons of 17 Black slaves were excavated from an unmarked 18th century cemetery in Montserrat, West Indies. A pharmaceutical phial found with one of the probable coffin burials bears the inscription OCT 29 1751. The date on the phial, skeletal analysis and ethnohistorical records suggest the skeletons are those of Black slaves, possibly from the nearby Bransby Plantation. Evidence of pathological conditions include enthesopathies, osteoarthritis, anemia, malnutrition, a high incidence of fractures and one possible case of lepromatous leprosy. Ages at death suggest that the adult females were outliving the males.

## INTRODUCTION

In 1979 a construction crew digging a house foundation and adjacent swimming pool on the western coast of Montserrat, West Indies, unearthed fragmentary bones in association with a historic bottle bearing a date of OCT 29 1751 (Watters, 1981). Construction halted and David R. Watters, a visiting archaeologist, was summoned to examine the skeletons. Watters identified the bones as human and belonging to more than one individual. A preliminary examination of the site revealed additional clusters of human bones. Although construction resumed, by the end of one week a total of 10 individual burials (1-10) and one multiple burial (probably commingled individual burials removed by the construction crew) had been excavated in an attempt to salvage as many skeletons as possible (Watters, 1987). Final analysis reveals that a minimum of 17 individuals (Table 1) were excavated.

The Harney site, so named after the building contractor, represents an unmarked and unknown (to the local inhabitants) Black slave cemetery in use during the latter 18th century (inclusive dates are unknown). Due to the paucity of recovered skeletons in the West Indies, little is known about the diet, disease, stature, nonmetric traits and dentition of Black slaves. The Harney site, therefore, offers researchers an opportunity to examine the skeletons of 18th century slaves of African ancestry (Williams, 1970).

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Table 1.—*Minimum number of individuals.*

Burial	Sex	Age	Race
1	F	50+	Indeterminate
2	F	20–30	Indeterminate
3	M	35–45	Indeterminate
4	F	60+	Black
5	F	50+	Indeterminate
6	F	18–35	Indeterminate
7	M	25–35	Black
8	F	40+	Indeterminate
9	M	40+	Indeterminate
10	M	35–45	Indeterminate
11	M?	18–40	Indeterminate
12	M	18–40	Indeterminate
13	M	18–40	Indeterminate
14	?	7–8	Indeterminate
15	?	8–10	Indeterminate
16	?	10–12	Indeterminate
17	?	14–16	Indeterminate

#### METHODS AND MATERIALS

A minimum of 17 individuals were recovered from the Harney site. The 10 individual burials each represent one adult (6 females and 4 males) while the multiple burial (single burials commingled by the construction crew) contains portions of at least 7 individuals (4 subadults and 3 adult males). The minimum number of individuals present in the multiple burial is conservatively based on a count of 4 left subadult femora and 3 left adult femora. There is, however, evidence of one additional subadult (maxilla and teeth indicate 13–15 years) as well as a very small female (60+ years) as evidenced by an innominate and two femoral heads (Table 2). The femoral heads measure 36 mm in diameter and are much too small to correspond to the 3 left femora identified as males. These two individuals were not included in the minimum number of individuals (MNI) reported. The multiple burial, then, contains the commingled skeletons of individuals of both sexes, ranging in ages from 7–60 years. No fetal or infant skeletons were recovered from the site.

The skeletons were received at the University of Tennessee in three boxes. Individual burials were packed separately from those of the multiple burial. Each individual burial was placed on a metal tray and tagged with the appropriate burial number assigned in the field. This facilitated examination of the skeletons and eliminated the possibility of mixing bones of two burials. During the laboratory analysis every effort was made to match elements in the multiple burial with the individual burials (numbers 1–10). In no instance were the authors able to crossmatch a bone in this manner. Burials 1–10 represent primary single interments with no evidence of commingling with the multiple burial (although Burial 9 was disturbed upon interment of Burial 1 [Watters, 1987]).

Bones in the disturbed multiple burial were sorted on the basis of intragroup size seriation, sex and age. The 4 subadult left femora (burials 14–17) were aged by comparison of size and length to an age-graded reference series. The adults were assigned burial numbers (11–13) following a detailed sorting of all elements that considered sex (size and robusticity), age (osteoporosis and degree of degen-

Table 2.—*Bones of the multiple burial indicating age and sex.*

Bone	Sex	Age	Race
1	F	60+	Indeterminate
2-3	F	60+	Indeterminate
4-5	M	Adult	Indeterminate
6	M	Adult	Indeterminate
7	?	20-30	Black?
8	F?	Adult	Indeterminate
9	F?	Adult	Indeterminate
10	F?	Adult	Indeterminate
11	F?	60+	Indeterminate
12	?	Adult	Indeterminate
19	M	30-40	Black

erative joint disease), morphological similarity and metrical analysis. By a process of elimination most of the bones were matched to specific individuals to the exclusion of others. Some elements, however, remain unmatched. For example, skulls in the multiple burial could not be reasonably matched with any of the postcrania, even if the bones were of similar color (soil discoloration), sex and age. Corresponding elements of the crania and postcrania were reconstructed to obtain measurements. In a few instances we were able to match femora with tibiae based on intragroup seriation and metrical analysis (this did not affect the MNI). No attempt was made to match unlike elements (e.g. arm with leg bones) unless morphological traits strongly suggested a match. Each bone was then inventoried on separate sheets denoting metrics, age, race (skulls), sex, completeness and pathological conditions. Although this is a time consuming method of analysis, it offers an appraisal of the general characteristics of each bone and individual in the sample (for a more detailed account of this method refer to Owsley et al., 1985a). The criteria used in estimating age, race, sex and stature consist of conventional methods used by practicing anthropologists. In instances of conflicting aging criteria the most reliable method was emphasized in the final assessment. For example, an individual with open cranial sutures and an eroded auricular surface (ilium) was aged by the latter. When dental attrition conflicted with degenerative joint disease the former was chosen. Most individuals, however, did not present such ambiguities.

Primary race estimates are based on those criteria exhibited in the skull (Bass, 1971). The shape, width and inferior border of the nasal aperture were given the most weight. Alveolar prognathism, dental crenulations (wrinkles), vertical subnasal corrugations (De Villiers, 1968) and general cranial contour were also considered. Of secondary importance were the criteria of femur curvature and the lack of shovel-shaped incisors.

Sex was determined by the shape and depth of the sciatic notch, maximum diameter of the femoral head, size of the mastoid processes, chin shape, browridge flatness, sharpness of the upper margins of the eye orbits, nuchal and supramastoid crest development, cranial size and shape, long bone seriation (intragroup) and comparison with known-sex skeletons.

Due to the fragmentary condition of the skeletons, stature could only be determined for 4 individuals (3 females and 1 male). Trotter and Gleser's (1952) formula for American Blacks was used. In most instances the long bones of the legs had to be reconstructed before measurements could be taken.



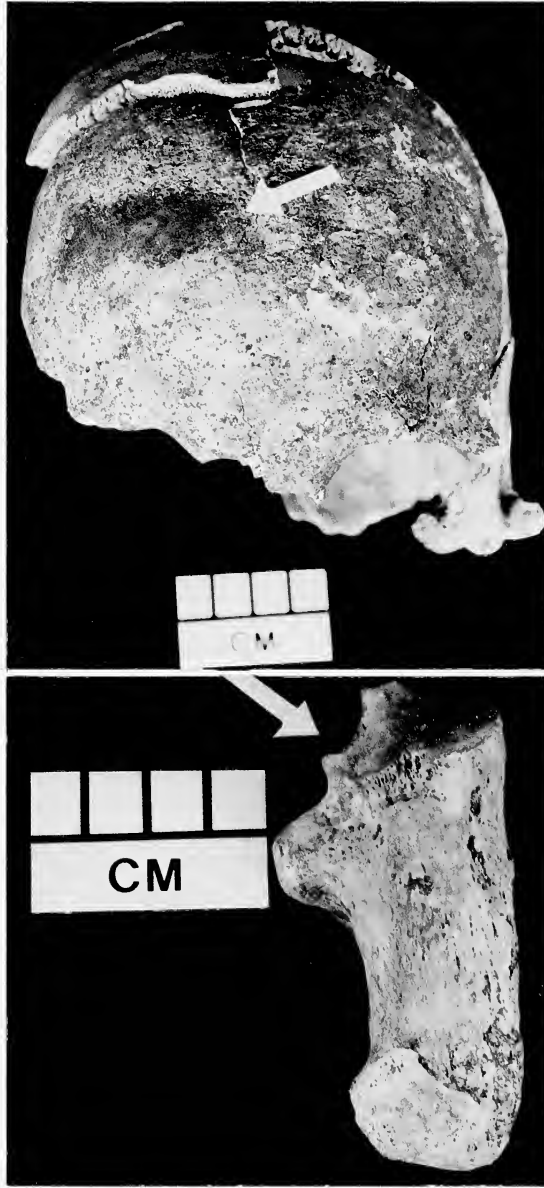


Fig. 1 (above).—Burial 2. Frontal view of skull showing copper salts stain.  
Fig. 2 (below).—Burial 3. Inferior view of left calcaneus (arrow points to secondary os calcis “notch”).

Paleopathological analysis is based on a three-category system designed to classify the bone cell response (to disease) present in the bone. The categories consist of bone loss (e.g. resorption, porosity), bone apposition (e.g. periostitis) or both. Each category has specific codes that further narrow and define the bone lesion according to severity, location (joint or nonjoint) and, in some instances, specific disease (e.g., lepromatous leprosy).



## BURIAL ANALYSIS

*In situ Burials*

*Burial 1.*—Female, race indeterminate, 50+, 5'1¾". This skeleton is in a fair state of preservation with the following elements present: both femora, tibiae, fibulae, right foot, fragmentary left radius, ulna, hand bones and innominates. Most of the arm bones and long bone ends are missing (post mortem). This female exhibits moderately robust long bones but a gracile radius and ulna. Female traits consist of a wide, shallow sciatic notch and a delicate ischium. Marked osteoporosis combined with porosis of the acetabula suggest old age.

Pathological Condition: The left hand exhibits a swollen and disfigured metacarpal, eburnated (polished) carpal, arthritic destruction of one distal phalanx and an osteochondritic pit in the greater multangular. There is an area of ossified connective tissue (enthesopathy) on the ventral surface of the left patella and posterior surfaces of the tibiae resulting from repeated physical stress. The right fibula exhibits a healed fracture near its midshaft. It is probable that this female favored her right leg following an injury, as noted by the slightly atrophied right femoral shaft. The midshaft circumferences of the femora are 8.5 cm (left) and 8.0 cm (right).

*Burial 2.*—Female, race indeterminate, 20–30. This fragmentary skeleton is in a poor state of preservation with the following elements present: most of the skull, mandible and teeth of both jaws, and a fragmentary left humerus, left femur and dens of the second cervical vertebra. Sex is based on the sharp orbital margins, a pointed chin, flat browridges, small mastoids, cranial shape and gracile long bones (Krogman, 1962; Bass, 1971; Stewart, 1979). Aging criteria consist of slight dental attrition, open cranial sutures, thick cortical bone and lack of degenerative joint disease. The overall size of the skeleton suggests a small female. There is a green copper salts stain on the right frontal bone suggesting a shroud pin or other ornament was buried with her (Fig. 1).

Pathological Condition: Slight erosion and porosity of the right mandibular fossa. Bilateral cribra orbitalia and slight porotic hyperostosis (Ortner and Putz-Char, 1981). The teeth exhibit slight attrition and no abscesses; 3 teeth are carious and present hypercementosis. Eleven teeth have enamel hypoplastic lines encircling the crowns.

*Burial 3.*—Male, race indeterminate, 35–45, 5'4". Both legs and feet are present (the upper skeleton was destroyed by bulldozers). Muscle markings, a femoral head diameter of 46 mm and large long bones suggest this individual to be one of the larger males recovered. The contour of the femora is relatively flat. An age of 35–45 is based on moderately thick cortical bone and only slight arthritic lipping of the proximal articular surface of the left tibia.

Pathological Condition: This individual presents a number of pathological lesions. First are the osteophytes on the articular surface of the distal right femur. Both tibiae exhibit superiorly directed bony projections (enthesopathies) on the tibial tuberosities. Two proximal foot phalanges exhibit severe osteoarthritis of the distal joint surfaces.

Anomaly: Both calcanei (although the right calcaneus is damaged a trace of the trait is still visible) exhibit evidence of what Dwight (1907) terms a secondary os calcis (Fig. 2, 3). This true accessory bone lies within the joint spaces between the calcaneus, talus, cuboid and navicular. The secondary os calcis is a small, roughly semilunar-shaped bone that is slightly convex along its medial border and convex

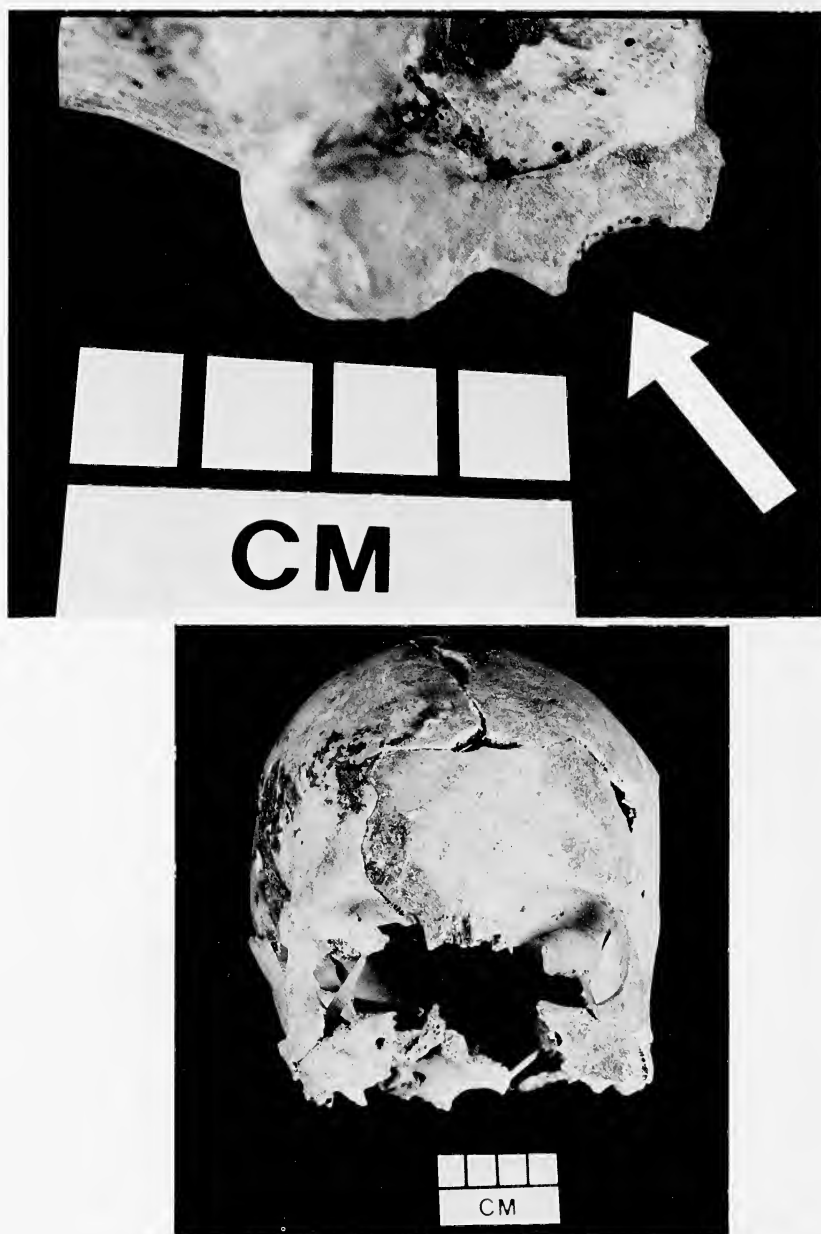


Fig. 3 (above).—Burial 3. Superior view of left calcaneus (close up of secondary os calcis "notch").

Fig. 4 (below).—Burial 4. Frontal view of skull.

at its lateral margin where it articulates with a "notch" in the anterior talocalcaneal facet. The presence of such a bone would not cause pain or discomfort. Although the frequency of this accessory bone (in skeletal and extant populations) is not known, preliminary research by one of the authors (RWM) shows it to occur in about 1 of every 8 individuals examined (general population).

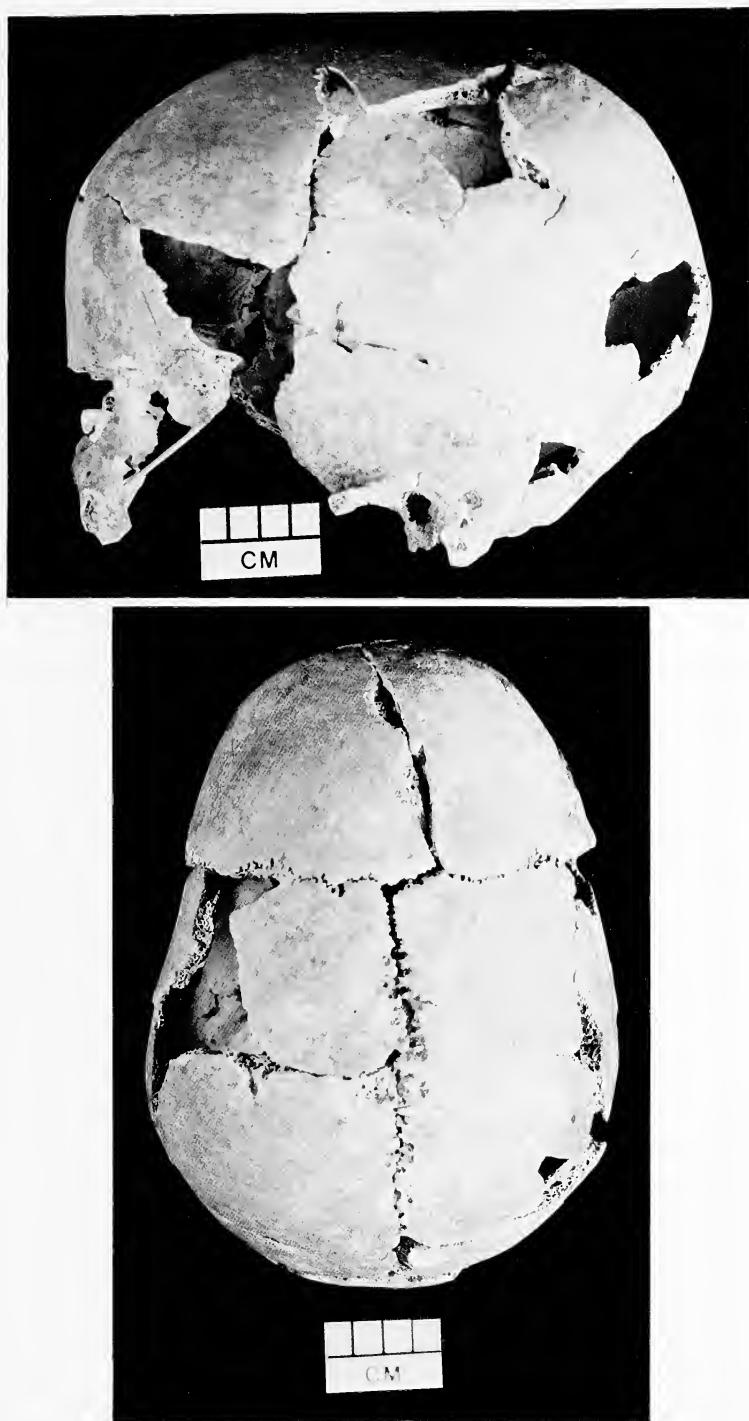


Fig. 5 (above).—Burial 4. Left lateral view of skull.

Fig. 6 (below).—Burial 4. Superior view of skull.

Table 3.—*Burial 4 cranial measurements (in millimeters).*

Glabello-occipital L	195
Nasion-occipital L	196
Basion-nasion L	115
Basion-bregma Ht	146
Maximum cranial Br	135
Minimum frontal Br	94
Biauricular Br	113
Minimum cranial Br	80*
Biasterionic Br	99
Mastoid Ht	23
Mastoid Br	10
Orbital Ht	32
Orbital Br	32
Bifrontal Br	90
Biorbital Br	91
Cheek Ht (minimum)	20
Supraorbital projection	5
Glabella projection	1
Frontal chord	122
Frontal subtense	29
Parietal chord	118
Parietal subtense	24
Occipital chord	98
Occipital subtense	23
Foramen magnum L	34
Foramen magnum Br	29*
Nasion radius	108
Bregma radius	135
Vertex radius	136
Lambda radius	119
Opisthion radius	41
Basion radius	12

\* Approximate measurement.

*Burial 4.*—Female, Black, 60+, 5'1/4". This female is the most complete individual recovered. The only elements missing are most of the ribs, sternum, portion of the maxilla and right pubis. Sex is based on the size and shape of the skull (Fig. 4–6; Table 3), flat browridges, small mastoids, pointed chin and a wide, shallow sciatic notch; note the small, rounded eye orbits in Fig. 4. Racial traits consist of nasal guttering and alveolar prognathism. Although the cranial sutures are open, an age of 60+ is based on the edentulous maxilla and mandible, marked osteoporosis, eroded symphyseal face, degree of osteoarthritis and auricular surface changes. There is a green copper salts stain on the left frontal bone.

Pathological Condition: Bilateral cribra orbitalia (Fig. 7). The endocranial surface of the frontal bone exhibits 3 or 4 small protuberances, often referred to as enostoses or Hyperostosis Calvariae Interna (Perou, 1964), probably of a benign nature. The innominates exhibit porosity in the acetabular surfaces and a small lytic lesion superior of the left acetabular rim. The left thumb (metacarpal) exhibits a healed fracture. The right patella and joint surface of the distal right femur are eburnated. The corresponding articular surfaces display deep grooves and erosion resulting from bone on bone contact (osteoarthritis). Based on the lack of long bone atrophy it is probable that this individual remained active until or near the time of her death. The most striking pathological condition seen in this skeleton is the marked degree of osteoarthritic changes in the femoral heads (Fig. 8). The

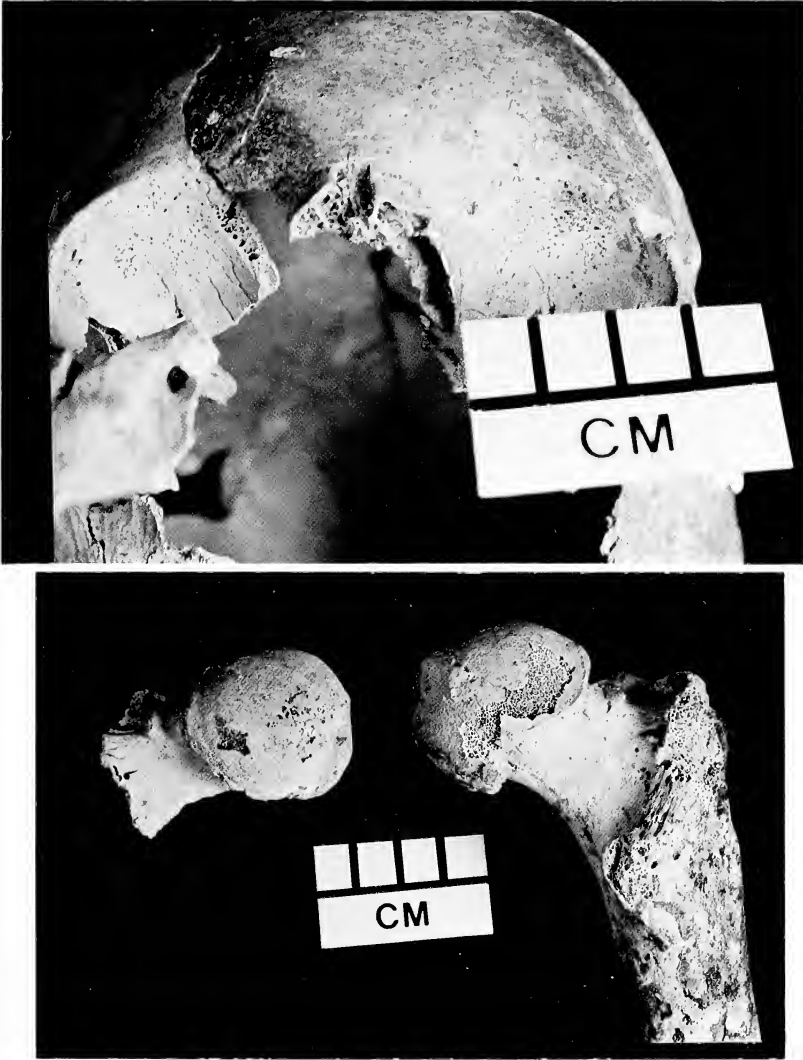


Fig. 7 (above).—Burial 4. Bilateral cribra orbitalia.

Fig. 8 (below).—Burial 4. Osteoarthritic femoral heads (posterior view).

surfaces exhibit porosity and new bone growth as well as periarticular mushrooming. The femoral necks appear normal in length but display small areas of bone apposition, possibly in reaction to hyperextension of the legs (Angel, 1964) or contact with the rim of the acetabula (Fig. 9, 10).

*Burial 5.*—Female, race indeterminate, 50+, 5'1". The skeleton is represented by both lower arms and hands, distal left humerus, 4 lumbar vertebrae, left innominate, both femora, tibiae, fibulae and feet. Sex is based on a wide, shallow sciatic notch, small long bones and femoral head diameter of 40 mm. Age is based on the degree of osteoporosis and auricular surface changes (Lovejoy et al., 1985).

*Burial 6.*—Female, race indeterminate, 18–35. This individual is represented only by the tibiae and a crushed right femur and fibula. Sex is based on the small

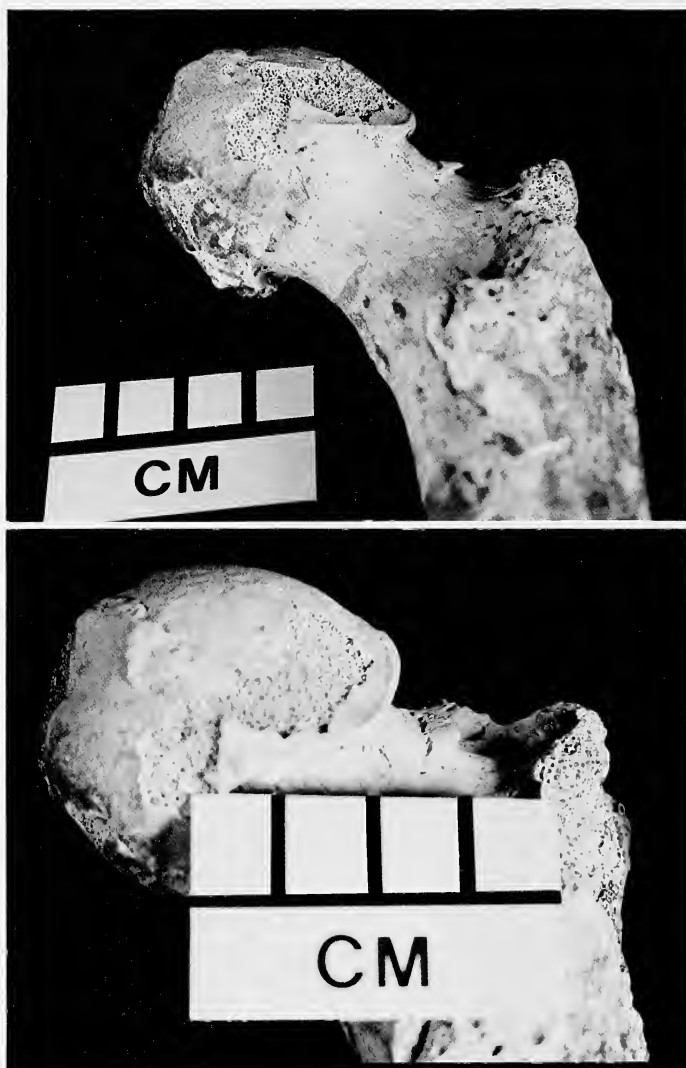


Fig. 9 (above).—Burial 4. Posterior view of right femur (note the small osteophyte extending from the neck).

Fig. 10 (below).—Burial 4. Close up of posterior right femur (porosity artifactual).

size of the tibiae and gracile muscle markings. Age is based on the adult size of the tibiae and thick cortical bone.

**Pathological Condition:** The distal right tibia exhibits a small area of nearly healed periostitis, possibly the result of acute trauma (fracture?).

**Burial 7.**—Male, Black, 25–35. The only elements present consist of a nearly complete skull (Fig. 11, 12) and mandible. Male traits consist of a well developed nuchal crest, intermediate mastoids, square chin and a large gonial angle with a wide ascending ramus. Because of the fragmentary nature of the facial region race is based on the general contour of the skull (R. L. Jantz, personal communication, 1986). The open cranial sutures, moderate dental attrition, obliterated incisive suture (Mann et al., 1987) and thick diploe suggest an age of 25–35 years.

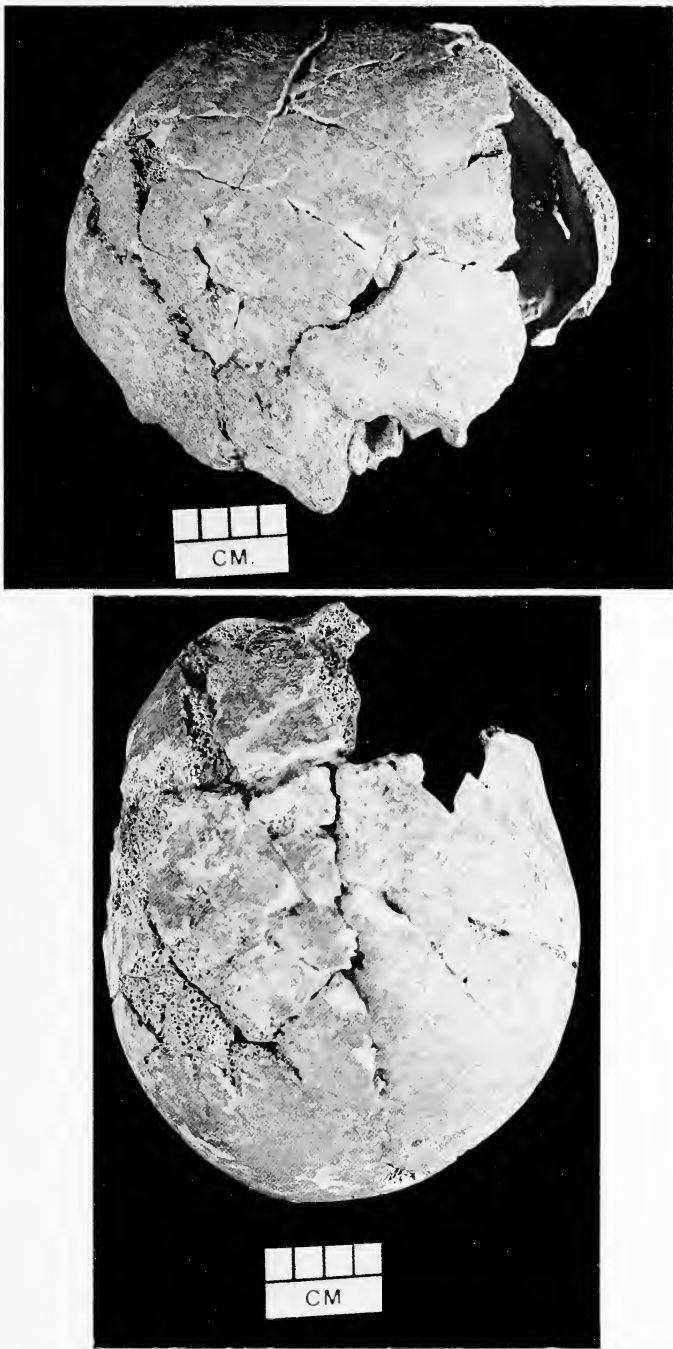


Fig. 11 (above).—Burial 7. Right lateral view of skull (portion of frontal bone is missing).  
Fig. 12 (below).—Burial 7. Superior view of skull.

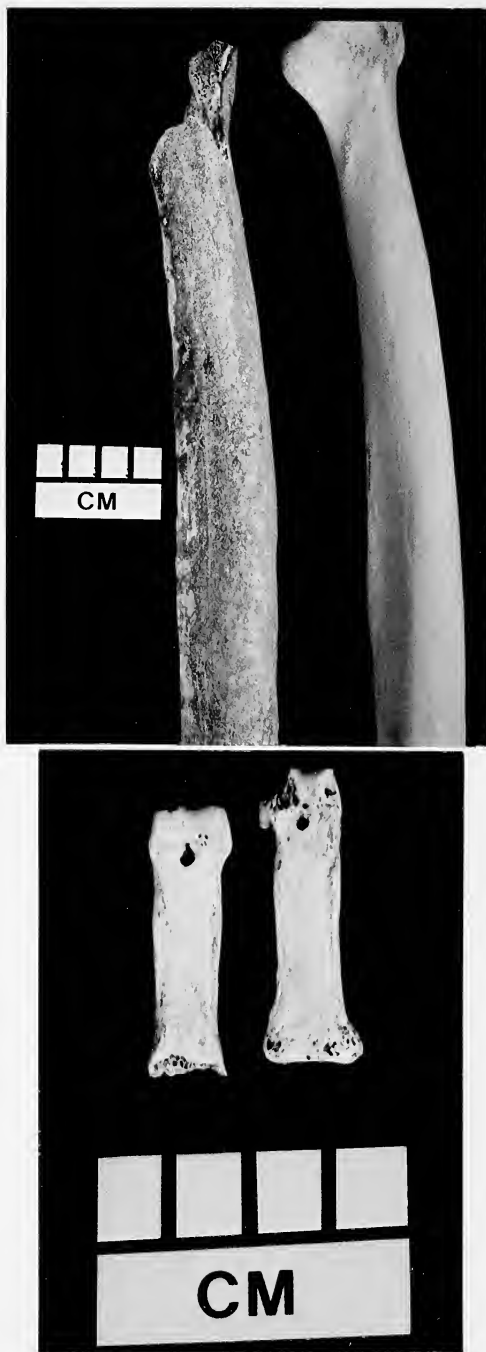


Fig. 13 (above).—Burial 9. Robust left femur in comparison to a known large adult male.

Fig. 14 (below).—Bones 14 and 15 (hand phalanges) of the multiple burial exhibiting enlarged nutrient foramina.



**Pathological Condition:** The right mandibular condyle displays slight erosion. Bilateral cribra orbitalia and slight porotic hyperostosis. Active endocranial porosity is visible in the frontal and parietals bordering the superior sagittal sinus. Enamel hypoplasias. There is a pipe-stem groove in the left mandibular canine.

**Anomalies:** The left maxilla exhibits a small supernumerary tooth (crown missing) on the buccal surface, interproximal of M<sup>2</sup> and M<sup>3</sup>. Another supernumerary tooth is present in the socket of the right mandibular incisor (two-rooted). A third small supernumerary tooth is present but the alveolus is missing. The mandibular central incisors present bulbous lingual cingula.

*Burial 8.*—Female, race indeterminate, 40+. This individual is in a very poor state of preservation and represented only by the shafts of the femora, a few long bone fragments and the left mastoid process. The extremely small mastoid and gracile femur strongly suggest female. Age is based on thin cortical bone and a rugged cortex.

**Pathological Condition:** The posterior surface of the right tibia displays a small area of porous, striated bone indicating active periostitis.

*Burial 9.*—Male, race indeterminate, 40+. This large male is represented by portions of the left femur, tibia and both ulnae. The left femur is extremely robust and measures 34 mm (anteroposterior) and 27 mm (mediolateral) at the midshaft (Fig. 13). The development of the aspera contributes heavily to the robust appearance. The right ulna is also robust. Age is based on the presence of marginal lippling of the olecranon fossa and thin cortical bone.

**Pathological Condition:** The left femur is the most robust bone in the sample and measures within the stenomeric range (103) on the platymeric index (Bass, 1971).

*Burial 10.*—Male, race indeterminate, 35–45. The only bones presented are the femora, tibiae and one left metatarsal. No articular surfaces survive. The generally smooth, thick cortex of the leg bones suggest middle age. Muscle markings are moderate indicating this to be a male of medium build (intragroup comparison).

#### *Multiple Burial (Disturbed by Construction)*

*Burial 11.*—Probable male, race indeterminate, 18–40. This individual is represented only by a portion of the left femur. This bone is intermediate in size and robusticity but fits better within the male range. The thick cortical bone suggests young to middle age.

*Burial 12.*—Male, race indeterminate, 18–40. Present only is the left femur missing both articular ends. This bone is moderate to robust and has a well developed linea aspera and thick cortex suggesting young to middle age.

*Burial 13.*—Male, race indeterminate, 18–40. Present only is the left femur missing both articular ends. This bone is also robust and exhibits a thick, smooth cortex suggesting a young to middle age adult.

*Burial 14.*—Subadult, 7–8. The only element present is a left femur, missing both articular ends. Based on intragroup seriation and comparison to a known-age femur this individual is 7–8 years of age.

*Burial 15.*—Subadult, 8–10. Elements present are both femoral shafts and tibiae. Intragroup seriation and known-age comparison suggest an age of 8–10. The right tibia exhibits active porosity over much of its surface.

*Burial 16.*—Subadult, 10–12. Bones present consist of fragmentary femora. The right femur exhibits a portion of the billowy epiphyseal surface for attachment of the head. Intragroup seriation places this child at 10–12 years.

*Burial 17.*—Subadult, 14–16. Present are fragments of both femora and tibiae.

This is the largest subadult in the sample. The right femur and tibia exhibit active periostitis.

*Bones of the Multiple Burial Indicating Age and Sex*

*Bone 1.*—Female, race indeterminate, 60+. This fragment consists of the right innominate with a wide sciatic notch and small acetabulum. The auricular surface is eroded and macroporotic suggesting an age of 60+.

*Bones 2 and 3.*—Female, race indeterminate, 60+. Both femoral heads (left measures 36 mm and the right 37 mm) are present and match. The small size of the heads and obliteration of the epiphyseal lines indicate this to be a small, adult female. The femoral heads fit the small right acetabulum listed above (Bone 1) and belong to the same individual.

*Bones 4 and 5.*—Left and right femoral heads (each 45 mm in diameter); size suggests this to be a good match and probably of the same adult male.

*Bone 6.*—Right femoral head (45 mm), adult male.

*Bone 7.*—Right maxilla and 5 teeth, adult. The shape of the nasal aperture suggests a probable Black (admixture?). Dental development and attrition suggest an age of 20–30 years.

*Bone 8.*—Portions of a skull (one individual). Active porotic hyperostosis of the parietals and occipital. This is probably a young adult female as evidenced by small mastoids processed and undeveloped supramastoid crests. Cranial sutures are open.

*Bone 9.*—Mandible fragment with a pointed chin, probable adult female.

*Bone 10.*—Mandible fragment with a pointed chin, probable adult female.

*Bone 11.*—Edentulous mandible, female 60+ (probably goes with the innominate and 2 femoral heads noted above).

*Bone 12.*—Right clavicle (adult) with a green copper salts stain.

*Bone 13.*—Numerous cranial fragments of one individual (sex and age indeterminate). Green copper salts stain on the left frontal bone.

*Bones of the Multiple Burial Exhibiting Pathological Conditions*

*Bones 14 and 15.*—Two middle hand phalanges with enlarged nutrient foramina (Fig. 14) suggesting lepromatous leprosy (Brothwell and Sandison, 1967; Steinbock, 1976; Donald Ortner, personal communication, 1986).

*Bone 16.*—One metatarsal with an oval-shaped lytic lesion in the diaphysis.

*Bone 17.*—One left metacarpal with a healed fracture of the diaphysis.

*Bone 18.*—Left ulna fragment with healed periostitis.

*Bone 19.*—Male, Black, 30–40 years. This maxilla (palate and 11 teeth only) is very large and exhibits classic Black features (Fig. 15, 16): a wide nasal aperture (27 mm), alveolar prognathism, vertical subnasal corrugations, nasal guttering, tapered central incisors, crenulated molars and a diastema between the central incisors. Age is based on slight dental attrition, erupted third molars and visible incisive suture. Carabelli's cusp is present.

Pathological Condition: Linear enamel hypoplasias and slight to moderate hypercementosis. Chronic osteitis of the right maxillary antrum (Fig. 17) due to a periapical abscess of the second premolar. The left first molar has a large occlusal caries. The mandibular premolars and molars exhibit large buccal wear facets. There were a few loose mandibular teeth recovered in the multiple burial that show corresponding wear facets on their lingual surfaces. This pattern of dental wear suggests that the mandible may have been much smaller than the maxilla.

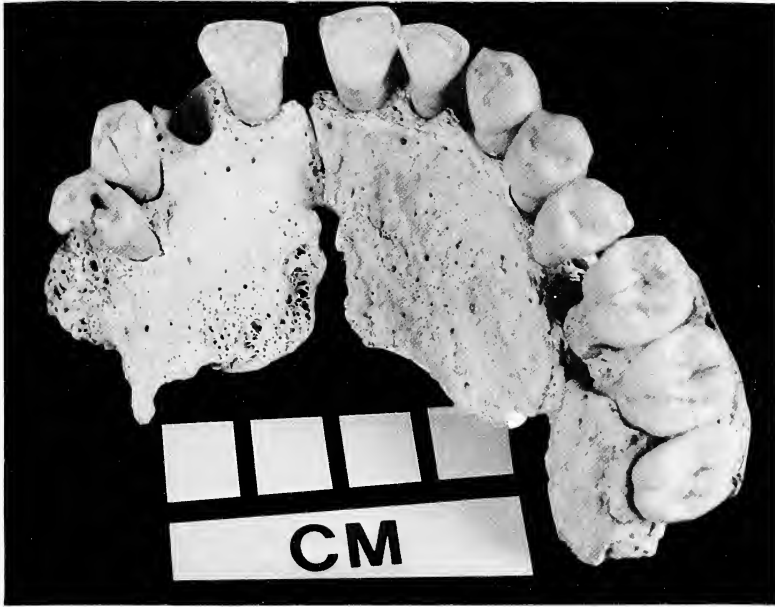
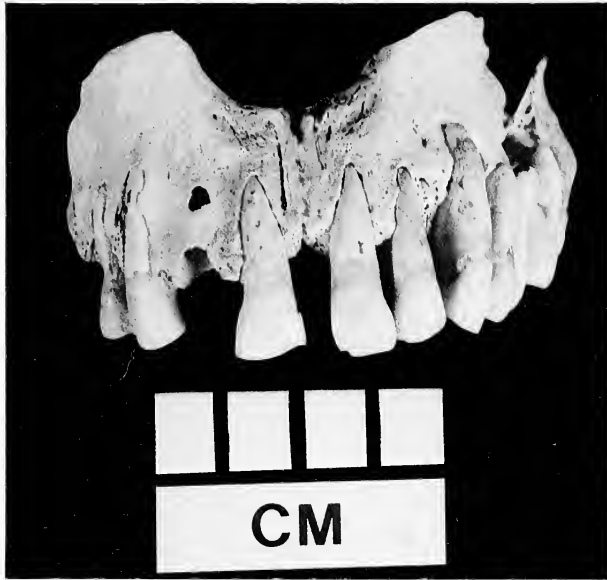


Fig. 15 (above).—Bone 19 of the multiple burial (maxilla of adult Black male; missing bone is artificial).

Fig. 16 (below).—Bone 19 of the multiple burial (lingual surface of maxilla).

Another possibility for the uneven wear is that pain associated with the periapical abscess may have caused the individual to favor chewing on the left side.

#### DENTAL SUMMARY

A total of 92 teeth (both loose and in sockets) were recovered from the site and include the following: 18 incisors, 13 canines, 27 premolars and 34 molars. Many

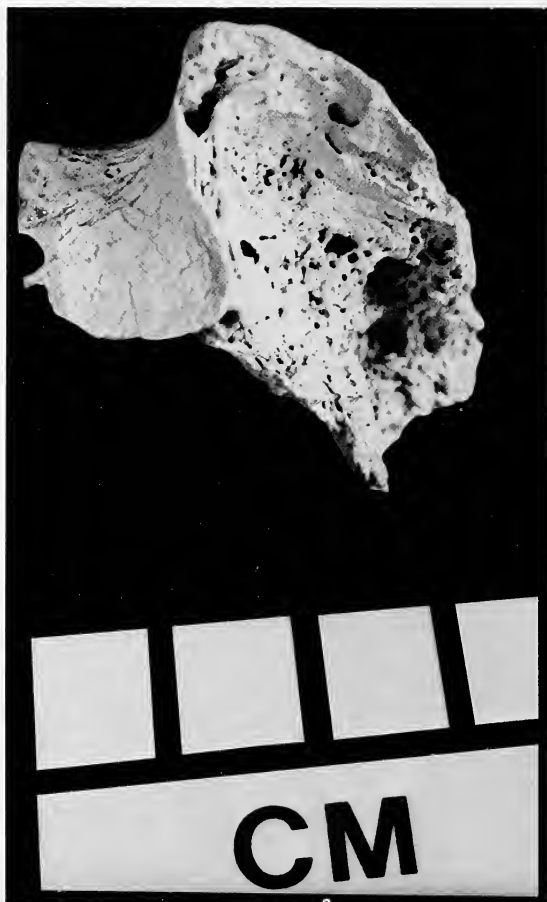


Fig. 17.—Bone 19 of the multiple burial (chronic osteitis of right antrum; note the thickened and porous appearance of the new bone).

of the teeth exhibit caries (17 of 92), root hypercementosis and enamel hypoplasias similar to those described by Corruccini et al. (1982, 1985), of a Black slave cemetery in Barbados. The frequency of dental caries by tooth type includes the following: 1 incisor, 1 canine, 8 premolars and 7 molars. Also present are 3 periapical and 1 periodontal abscesses. Two individuals exhibit pipe-stem grooves. In this small sample there is no evidence of intentional tooth mutilation or shovel-shaped incisors.

In general the teeth reflect a moderately high fiber diet resulting in a slight to moderate dental attrition. The high frequency of dental caries (18%) may reflect a diet high in natural sugar, possibly from chewing sugar cane (Owsley et al., 1985b). Dental attrition and wear patterns of this sample do not reflect a rough, gritty diet as seen in prehistoric Amerindian groups. The dental wear patterns of this group represent a diet between the abrasive diet of the Amerindian and the refined diet of the more industrialized peoples.

#### DISCUSSION AND SUMMARY

Final analysis suggests that the skeletons examined are those of Blacks, possibly slaves from the nearby Bransby sugar plantation. The lack of fetal and infant

skeletons supports the findings of other researchers that Black slaves were selectively burying their dead in particular sections of the cemeteries, if not elsewhere (Corruccini et al., 1982). Construction deadlines at the Harney site precluded a thorough excavation of the entire cemetery which would have allowed for a more accurate rendering of slave mortuary practices in Montserrat. It is likely, however, that the burial practices at the Harney site were similar to those deduced by Corruccini et al. (1982).

The males in the Harney site sample are moderate to robust in build yet short in stature and differ from the historical description of the "best slave" as being 5'11" (Williams, 1970). The stature of the three measurable females clustered around 5'1". A general comparison of Harney femora and tibiae with known-sex and -race individuals suggests generally taller but less robust than the Amerindian sample (Arikara of the Northern Plains), and shorter but more robust than the White sample (forensic cases). Development of the linea aspera (femur) and a greater anteroposterior diameter are distinguishing features of the Harney skeletons.

Due to the fragmentary nature of the skeletons only 3 individuals could be reliably raced (Black; a fourth individual exhibits Negroid traits but not as strongly as the others). The general contour of most femora (anteroposteriorly) is flattened, further suggesting Black individuals.

The age distribution by sex presents an interesting pattern. Five of the 6 identifiable males were less than 45 years old at death and the sixth 40+ years. The females, on the other hand, outlived the males in this sample; of the 6 identifiable females 4 are 40+ and only 2 died in their thirties.

Most of the Black slaves brought to the West Indies were either bought or captured on the coast of West Africa. Fully 16% of the slaves died aboard ships during "middle passage" and another 33% within three years of their arrival in the West Indies (Williams, 1970). Since there was little value in bringing older slaves to work on the plantations, the presence of old females suggests that they had survived as slaves for many years (not necessarily on Montserrat). Further research to detect the presence and amount of lead present in the bone may help clarify this question (Handler et al., 1986). The subadults, on the other hand, may have either been brought to Montserrat from Africa or were born on the island. The 5 subadults identified in this sample comprise nearly 30% of the individuals recovered from the Harvey site.

The overall disease pattern reflects a high frequency of anemia as evidenced by cribra orbitalia and porotic hyperostosis. Although present in a few individuals, periostitis doesn't appear to have been a major problem among these people. The most interesting disease noted in this sample is the presence of enlarged nutrient foramina (2 hand phalanges) suggestive of lepromatous leprosy. The lack of other diagnostic evidence precludes a firm diagnosis of the disease.

Another point of interest is the relatively high frequency of fractures in this group: 3 females (burials 1, 4, and 6) as well as an unprovenienced metacarpal in the multiple burial. It is interesting to note that fractures are identified only with the females.

The incidence of degenerative joint disease is moderate and seems to fit the expected scenario that joint involvement increases with age, probably commencing sometime in the late twenties. In only one individual is there evidence of severe osteoarthritis, this being in the right knee and hip. The sacra, innominates and few recovered vertebrae are relatively free of osteophytosis and osteoarthritis. Muscle attachment sites are also nearly free of enthesopathies which suggests that

these individuals were not engaged in prolonged activities that produce ossified connective tissue in the extremities.

Examination and measurements of the hand bones suggest these individuals had long, slender fingers in comparison to a sample of Amerindians and Whites. The hands appear to have been subjected to arduous grasping activities, as evidenced by the developed muscle attachment areas in the phalanges and metacarpals of the 5 individuals with recovered hands or feet; 4 individuals exhibit one or more of the following pathological conditions: osteoarthritis, healed fractures and volar curvature. Speculations concerning the bony changes present in these individuals are of little substantive value due to the small sample size.

In conclusion, the skeletons of at least 17 Black slaves consisting of 6 adult females, 6 adult males, 1 probable male and 4 subadults were recovered from the Harney site. Although the ratio of males to females is even, the males appear to have died at earlier ages, possibly reflecting a harsher and more disease prone lifestyle. Although excavation of the entire cemetery was not possible, the lack of fetal and infant skeletons suggests a selective burial pattern. The frequent occurrence of fractures, cribra orbitalia, porotic hyperostosis and enamel hypoplasias suggests that these individuals suffered the effects of periodic severe malnutrition, common illnesses and a harsh lifestyle that resulted in the early deaths of the plantation males.

#### ACKNOWLEDGMENTS

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**Abbreviations.** Refer to the CBE Style Manual for correct abbreviations. Mammalian dentition: use capital letters (I, C, P, M, D, for incisor, canine, premolar, molar, deciduous, respectively) and superscript/subscript numbers ( $M^2$ ,  $P_3$ ) to designate upper and lower teeth.

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**Illustrations.** All illustrations will be called figures, and are to be numbered in Arabic numerals. Three sets of illustrations are required, one (original artwork) for reproduction, two for reviewers. Xerox copies of photographs for reviewers are usually not acceptable but are adequate for line drawing review copies. All illustrations must be reducible to a maximum of 127 by 195 mm (30 by 46 picas) without loss of clarity. Line copy should be designed for reduction to  $\frac{2}{3}$  or  $\frac{1}{2}$  of actual size. Type-written illustration copy will not be accepted. Photographic figures should be submitted at **actual reproduction size**.

Two or more small figures should be combined for reproduction as a unit or plate, but, if feasible, do not combine halftones and line drawings. Rectangular halftone figures should be abutted, without intervening spaces. The printer will insert narrow white spaces during the reproduction process. Halftone figures with solid black backgrounds will not be accepted unless the author agrees to pay for the printing costs. All plates must have **minimally** one inch borders all around. Each plate should be given a protective cover and identified on the back side.

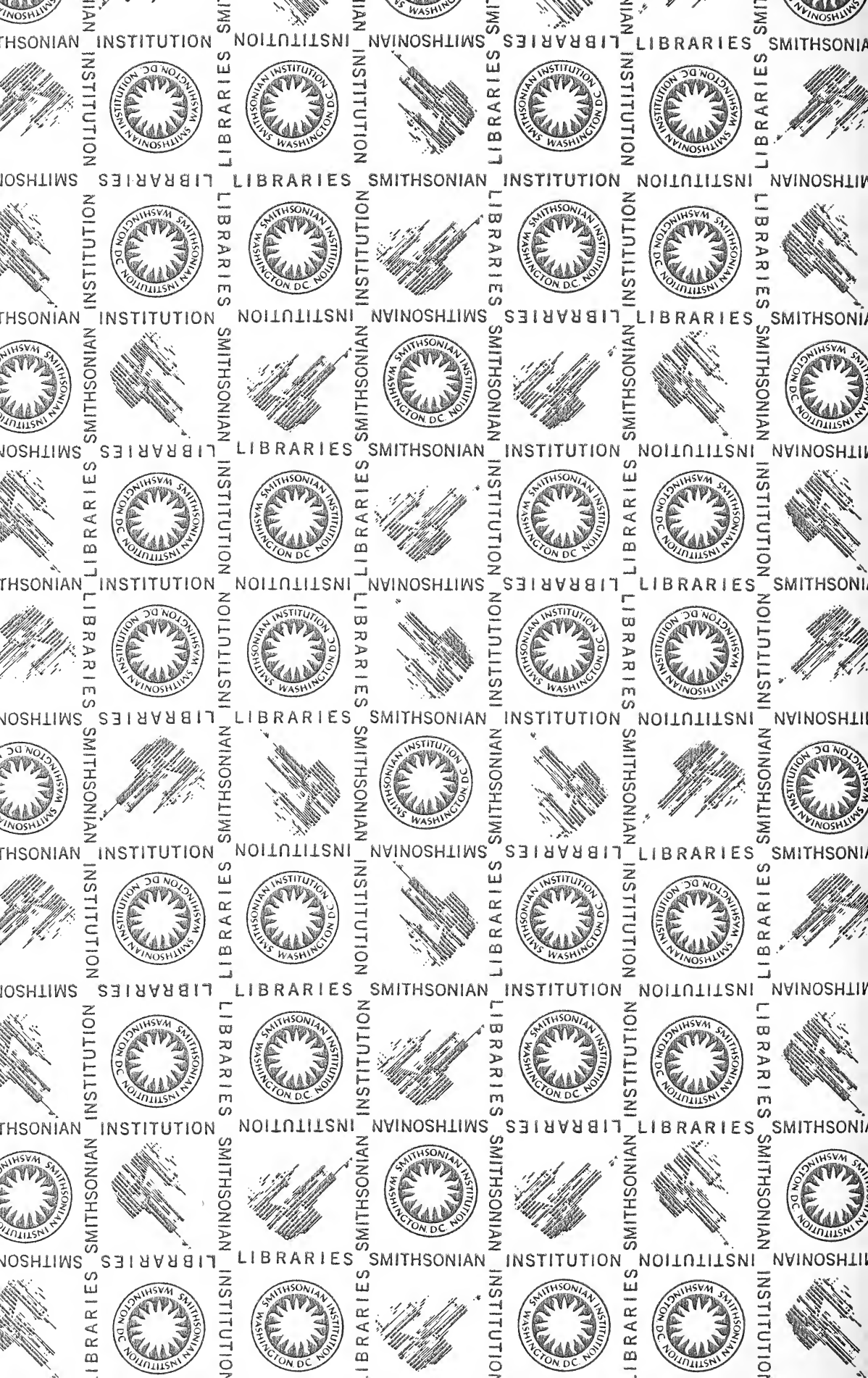
Lettering and/or a magnification scale (linear metric scale) for rectangular halftone figures should be placed directly on the photo, not in a blank space between photos. The scale or lettering for closely cropped photos can be placed in blank areas close to the figure.

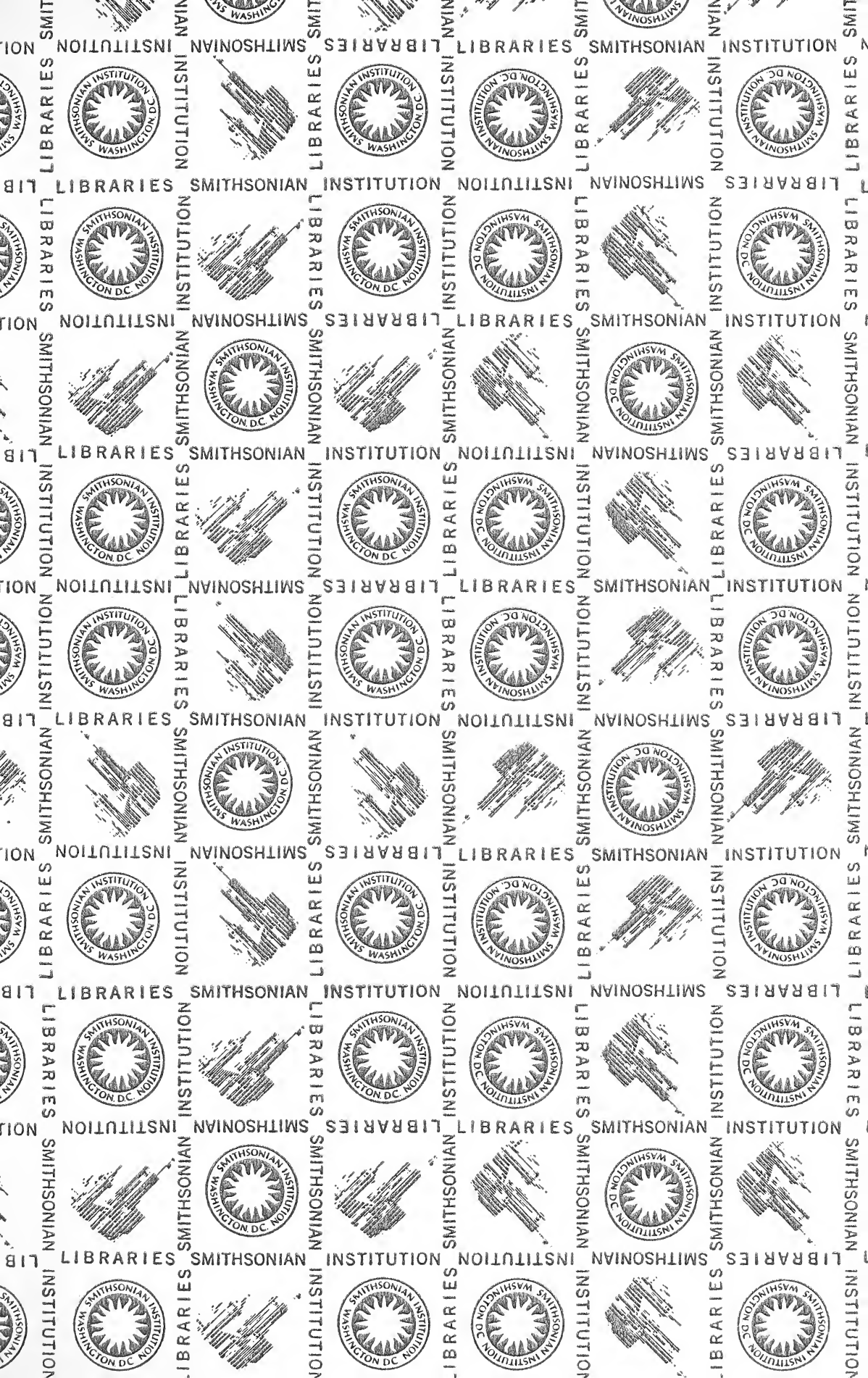
**Proof.**—The author should answer all queried proof marks and check the entire proof copy. Return corrected page proof with the edited manuscript **promptly** to the editors.

If an author chooses to make extensive alterations to a paper in proof stage the author or appropriate section will bear the cost. Original manuscripts will not be returned unless requested. Illustrations will be returned to the author.











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